The Functional Architecture of Interval Timing

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This thesis is dedicated to my mother.

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DECLARATION

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ABSTRACT

The following set of experiments investigates the fundamental mechanism proposed to underlie interval timing and addresses a key question in timing research pertaining to the underlying functional architecture. Numerous models have been proposed in an attempt to illustrate and explain timing performance, some based on dedicated features employing a specialised mechanism, whilst others suggest that time perception is inherent in neural dynamics. An influential set of models posit that the brain contains a mechanism akin to a mental stopwatch which can be started, stopped and paused at will. This premise was tested in the first experimental chapter, the expected decline in performance was calculated in line with model predictions. The observed deterioration significantly exceeded the calculated predictions indicating that human timing is not akin to that of a 'stopwatch' when timing short durations and is incongruent with the predictions of a pacemaker accumulator type mode that can be paused at will. Psychophysical methods have revealed that interval timing conforms to a fundamental property in sensory processing known as Weber's Law. Lawful relationships such as these are important because they inform and constrain models of human interval timing. The adherence to this property was investigated across a range of durations using two comparable tasks in the following experiment. Although violations across certain durations were observed, these were not mirrored in both the utilised tasks to a statistically significant degree. The results could tentatively be argued to suggest certain constraints on the scalar model albeit a firm conclusion cannot be asserted. The second question pertaining to multimodal processing across a range of tasks and durations, indicative of the underlying architecture of interval timing, (i.e. 'one clock or many') was addressed via transfer of learning and correlation in the two final experiments. Perceptual learning and the generalisation to untrained durations and temporal tasks was assessed in the first of these two chapters. Training was observed to improve performance at a few of the practised durations with a more global improvement for one participant across untrained durations. Generalisation to the motor tasks from the perceptual task was observed consistently in two of the longer trained durations for all three participants pointing to a partially shared or overlapping interval timing structure. The next study further addressed some of the dichotomies reported in timing literature, with a key focus on explicit and implicit timing. Particular attention was also bestowed on timing in language: the language task based on phoneme closure duration and not overly reliant on contextual cues was observed to have a significant association with both motor and perceptual timing tasks. The results of the conducted experiments when taken together point to independent mechanisms which nonetheless possess a significant overlap.

CHAPTER 1 – INTRODUCTION

1.1 Thesis Summary

The functional architecture and the core mechanism underlying our ability to time short intervals ranging from milliseconds to minutes have been extensively debated. A variety of methodological approaches have been employed to investigate these temporal mechanisms and processes. Psychophysical methods have been at the forefront of interval timing research and this is the approach which will be utilised in the following experiments. In order to provide a more complete depiction of interval timing research, the reviewed studies which serve as the foundation for this thesis will cover a wide array of techniques and procedures.

The scalar property described in detail in the following sections, is a key feature of the timing of short interval durations. It serves as the foundation for a number of models which illustrate temporal processing. Any deviations from this law could be revealing of the involvement of additional timing processes. Likewise they could be a potential indicator of the incompleteness of some of the more traditional models of interval timing. The first two experimental chapters look at certain predictions made by the more traditional models of interval timing and seek to reveal any discrepancies which may be associated with the scalar property.

A key question in timing research pertains to the functional architecture underlying interval timing – do we possess a single clock able to account for all timing behaviours in a variety of contexts, or is interval timing supported by a more distributed network, whereby different neural substrates and mechanisms govern timing depending on the duration and context? The final two experimental chapters aim to explore this by utilising a battery of tasks designed investigate the commonalities between motor and perceptual timing and the timing of different durations. The association between timing in language and other forms of timing in addition to implicit and explicit timing is the focus of the final experimental chapter.

1.2 General Introduction

Our ability to perceive and process time facilitates an extensive array of cognitive and motor behaviours; decision making, anticipation of action, accurate speech perception and the planning and execution of motor actions, are just a few features which rely on our sense of time. In short, we could say that timing is essential to the everyday activities we engage in, a fundamental feature of our existence. Ranging from circadian rhythms which operate over a twenty four hour cycle and govern metabolic and reproductive processes, to millisecond timing essential for language and motor control, an organisms' capacity to deal with a variety of timescales enables goal accomplishment and its successful survival.

Time can be described and understood as a sequence of events, a series of interval durations consisting of arbitrary periodicities. Episodic memories which allow humans to remember when a particular event occurred, are closely linked to the recollection of the order in which these temporal events took place. Animals too, display an ability to utilise

series of events in order to complete set objectives. ‘Episodic-like-memories’, associated with event sequences lasting from hours to days have been best exemplified by foraging studies with Scrub Jays (Clayton & Dickinson, 1998; 1999; Clayton, Yu & Dickinson, 2001) although the extent and prevalence of this level of cognitive processing throughout the animal kingdom has not yet been fully settled.

The well-known experiments conducted by Russian physiologist Ivan Pavlov (1849-1936) were among the first to discuss event timing in animals. Pavlov’s work on the inhibition of delay, revealed that the duration between the conditioned stimulus (CS) and the unconditioned reflex regulates the conditioned response (Denniston, Cole & Miller, 1988). In other words, after the presentation of the CS (which could be long or short) Pavlov’s salivating dogs were able to delay salivating until just prior to the onset of the unconditioned stimulus (US). Further advancement in the understanding of animal timing behaviour came from Skinner (1938) who developed the fixed interval procedure (a form of instrumental conditioning) whereby similarly to the ‘salivating dogs’ scenario, the reward is contingent upon a set amount of time passing after a given response. Since then numerous experiments have confirmed more sophisticated temporal abilities by animals, both innate and learned, which reveal their ability for timing short interval durations. Relative timing accuracy in interval duration perception has now been noted across many species, amongst them; “cats, rats, wood mice, pigeons, turtle doves, Tilapia (a fish species), and freshwater turtles” (Lejeune & Wearden, 1991, pg 84). Naturally this list simply exemplifies the ubiquity of interval timing in nature and is far from all-embracing.

Although there are other timing mechanisms which are available to animals, the circadian and interval ‘clocks’ have generally been the main focus of timing studies. There is evidence of interplay between these two ‘clocks’. For example, the duration of reproduced intervals has been found to vary depending on the circadian phase in both

humans (Aschoff, 1998; Kuriyama et al, 2005) and animals (Shurtleff, Raslear & Simmons, 1990). Furthermore dopamine (DA) is involved in both the regulation of circadian rhythms (Witkovsky, 2004) and the modulation of 'interval clock' speed (Matell & Meck, 2004; Matell, Bateson & Meck, 2006; Meck & Lake, 2013). However, it is generally assumed that these two 'timekeepers' utilize distinct neural mechanisms and processes (e.g. Hinton & Meck, 1997; Lewis Cordes & Gallistel, 2008). The focus of this thesis will be solely on the less understood of these timekeepers – interval timing, which refers to the approximation and reproduction of relatively short periods of time ranging from milliseconds to minutes.

Studies attempting to fully elucidate the mechanisms behind our ability to perceive and estimate short intervals of time, have covered a wide variety of approaches and methods. The field has greatly benefited from the development of research methods more revealing of possible timing physiology such as neuroimaging, despite these methods sometimes generating conflicting results (Meck & Malapani, 2004). Lesion studies conducted with patients who possess timing deficits have attempted to isolate the neural regions which may underlie timing. Similarly, research conducted with patients suffering from a variety of neurological disorders such as schizophrenia (Carroll, O'Donnell, Shekhar, & Hetrick, 2009; Davalos, Kisley,& Ross, 2002, 2003; Davalos, Kisley, Polk & Ross, 2003; Davalos, Kisley & Freedman, 2005), autism (Allman, DeLeon & Wearden, 2011; Szelag, Kowalska, Galkowski & Pöppel 2004) and of particular significance, Parkinson's disease (Pastor, Artieda, Jahanshahi, Obeso, 1992; Smith, Harper, Gittings, & Abernethy, 2007; Piras, Piras, Ciullo, Danese, Caltagirone & Spalletta, 2014) which is known to involve a degeneration of dopaminergic neurons in the basal ganglia, have greatly contributed to our understanding of temporal processing. Pharmacological studies too, have played a meaningful role, for instance by further substantiating the significance of effective dopaminergic activity in temporal processing. Nonetheless, psychophysics and

behavioural research, dating back to Vierodt's work on time perception in 1868, maintains its validity and is of considerable significance in clarifying the processes involved in interval timing. It has provided the backbone which fuelled the rise of modelling and physiological investigations.

In the following sections, I turn to the fundamental properties of time perception as revealed by psychophysics, and provide a brief description of a few of the current and influential models of interval timing. The observed disparities between different timing behaviours and durations, as well the implicit timing utilised by language, will be looked at in the context of the current evidence. Finally, an overview of the experiments that I have carried out, which make up the subsequent chapters, will form the conclusion of this chapter.

1.3 Weber's Law and the Scalar Property

Interval timing has been noted to display particular properties. Weber's Law, ubiquitous in sensory processing research, has also been found to apply to timing. Weber's Law specifies by how much a second stimulus must vary from the first in order for the two to be discriminated. In the field of time perception, it illustrates the proportionality between the mean and standard deviation of a timed stimulus (Hills, 2002).The scalar property is generated by timing behaviour and refers to the way in which the mean and standard deviation of the response distribution covary. In other words there is a linear relation between the obtained variability and stimulus duration, so that as the interval duration increases so does the standard deviation; this is known as the scalar property (Gibbon, 1977). Weber's Law has been supported by data in a variety of timing and time perception studies. The Weber Ratio, whereby the coefficient of variation (CV) equals the standard deviation (σ) over the mean (*t)* can be used in measuring and comparing

discriminability in timing data, and when the ratio remains constant, Weber's Law can be said to hold.

$$\mathbf{CV} = \frac{\sigma}{t} \qquad 1.1$$

Interval discrimination of a temporal interval is often evaluated using a fixed interval schedule of reinforcement whereby different stimuli can be utilised to reinforce a specific duration. A fixed interval schedule of reinforcement occurs where the first response after a criterion interval is reinforced. This is related to the peak procedure whereby fixed interval trials, which as noted above reinforce a criterion duration at the time of response, and peak interval trials where although a subject is expected to respond at a particular duration, the trial is not terminated with a reward at that point, are intermixed. Peak interval trials thereby map out a full distribution of responses, mirroring the animal's temporal expectation. An early fixed interval study was conducted by Dews (1970) who plotted the response rates of pigeons (using the following reinforcement values; 30s, 300s & 3000s) and found that the curve of cumulative responses as a function of *normalised* time (the time is expressed in proportion to the point of reinforcement) was the same irrespective of absolute duration, consequently denoting Weber's Law and the scalar property (i.e. timescale invariance) in timing. Catania (1970), also using pigeons but a very different methodology, found that the ratio of the standard deviations to the mean (coefficient of variation) remains mostly constant at different interval magnitudes. Allan and Kristofferson (1974) noted that the coefficient of variation over a certain temporal range (approximately 1000ms) remained unchanged. However, durations of less than 250ms appear problematic in the context of these studies, and it has been stated that rather than decreasing at a proportional rate the variability intersects the y-axis at a nonzero value (Fetterman & Killeen, 1992). This is sometimes

described as a near miss to Weber's Law, and implies the existence of some processes that contribute the same amount of variance to interval judgements regardless of duration. However, as the duration increases, their contribution becomes less noticeable and Weber's Law is observed.

Despite general adherence to Weber's Law, several studies have suggested a duration range at which optimum sensitivity is noted (e.g. Drake & Botte, 1993; Friberg & Sundberg, 1995). To test whether such a measure exists, Grondin, Oullet and Roussel (2001) evaluated five standard durations ranging from 500ms to 740ms using both visual and auditory stimuli and, unlike the two previous studies mentioned above, didn't observe a lower Weber Ratio for a specific duration in either modality. The authors suggest that the previously noted violations of scalar timing are likely due to the utilised methodology or individual preferences, although they don't eliminate the possibility that optimal timing could hold for shorter (e.g. <500ms) or longer (>0.740ms) intervals as is consistent with some previous literature. The ubiquity of Weber's Law in timing will be discussed in greater detail in Chapter 3.

Weber's Law is said to parallel the conversion of a sensory stimulus into an action potential which is then integrated in the central nervous system. Unlike in other sensory research, in the field of time perception, the nature of the stimulus is difficult to pin down as is the locality of this conversion (Matell & Meck, 2004). Weber's Law is not necessarily restricted to the study of perception, as studies looking at signalling pathways have noted that cells may sense the signal in a relative rather than absolute manner, a fold change which corresponds to Weber's Law (Goentoro & Kirschner 2009; Goentoro, Shoval, Kirschner, & Alon, 2009; Shovala, Goentorob, Harta, Mayoa, Sontagc, & Alona, 2010). Goentoro et al. state that with a signal which is continually repeating, relative

sensing allows cells to maintain the required level of sensitivity due to their constant adjustment to a background level without the need for a reset.

1.4. Models of Interval Timing

Despite a growing body of research, no consensus on the temporal mechanism responsible for processing temporal information in the interval range has been reached. However, numerous models have been suggested. These generally comprise of several stages which are thought to match the information processing which takes place in the perception and estimation of short intervals. Stages include the nominal 'clock stage' which enables an organism to record a certain duration, featuring an onset, offset and sometimes a reset, a 'memory stage' whereby particular durations are stored and referenced and a 'decision stage' which allows for comparisons to already encountered durations. Following is a brief summary of a few of the more prominent and influential models of interval timing.

1.4.1. Scalar Expectancy Theory

The Scalar Expectancy Theory (SET) proposed by John Gibbon (1977) and then further developed by Gibbon, Church and Meck, (1984) provided the current dominant template for our understanding of timing processes. SET was initially proposed as an extension of Weber's Law and a crucial aspect of it pertains to the Weber Ratio remaining constant over a wide scope of durations. Animal studies have provided a framework for SET, although many of the methods have since been adapted to investigate timing in humans.

The theory itself is based on the premise of a so-called internal clock or clock counter device (Gibbon, 1977, 1991) with properties akin to a stopwatch, whereby it can be

paused and restarted on demand. This model bears a significant similarity to a model proposed by Treisman in 1963, and features the same fundamental components which make up the general timing mechanism, although differences remain, particularly as to where the scalar property emerges. In its most basic form, the internal clock model posits a pacemaker which generates a series of pulses (units of time) which are sent to an accumulator and are stored whilst the switch is closed. The collected pulses are said to correspond to the amount of time which has passed, so that when an interval comparison is required, the pulses are counted by the accumulator and passed to a short-term memory store where a comparison with a specific duration can be made. The clock mechanisms have been noted to be generally quite flexible; they extend to include a wide range of time scales, but this is achieved at the cost of precision which could vary anywhere between 5% and 60% of the timed interval (Malapani & Fairhurst, 2002). This variability has been noted to reflect the uncertainty or noise which is proportional to the magnitude of the interval being timed. The subjective duration of each interval introduces a corresponding proportional error at any given range.

Despite the rise of alternate timing models in recent years, the internal clock model remains a relatively prominent feature in the field of temporal research, most likely due to its flexibility which allows it to encompass a wide range of timing behaviours. The model has enabled the interpretation of many experimental observations, although these mostly stem from psychophysical data (Church, 1984; Rammsayer & Ulrich, 2001) whilst additional physiological evidence supporting the model is sparse (Buhusi and Meck, 2005). Likewise, behavioural evidence obtained from animal studies supporting the linear representation of time (a fundamental aspect of the pacemaker-accumulator models) has also been challenged (Staddon & Higa, 1999). In order to accommodate the observed timing behaviours the internal clock model has had numerous adaptations and ad hoc additions. Most importantly it has been noted that the scalar property only emerges in the

stopwatch architecture through the inclusion of a multiplicative transformation which introduces Gaussian noise between the accumulator and short-term memory store (Staddon & Higa, 2006).

1.4.2. Adaptive Control of Thought – Rational Model

Taatgen, Van Rijn and Anderson (2007) have proposed a variant based on the internal clock model whereby timing is an added component of an already existing theory of cognition known as the Adaptive Control of Thought – Rational (ACT-R; Anderson & Lebiere, 1998, Anderson, Bothell, Byrne, Douglass, Lebiere & Qin, 2004). Within the original framework of the ACT-R architecture, time-keeping is only possible through explicit enumeration which is an unlikely representation of actual timing processes. Through the addition of a temporal module, which parallels the neural mechanisms as proposed by Matell and Meck (2000), the model retains the basic features of the 'stopwatch' whilst allowing for biological plausibility. The module is said to function independently of the cognitive structure with the only convergence occurring at the accumulator stage where a comparison of the resulting duration can be made. Within the clock module, the intervals between the pulses increase with duration, allowing the scalar property to emerge without further ad hoc additions. Duration estimates correspond to the amount of pulses stored in the accumulator and the gradually slowing pacemaker results in less precise estimates as intervals get longer. The representation of durations within the model is based on instance theory (Logan, 1988) which states that each experience, is stored in declarative memory. Memory and timing have been noted to rely on the same neural mechanisms and structures (Gu, Van Rijn & Meck, 2015; Lustig, Matell & Meck, 2005). Furthermore, Van Rijn, Gu and Beck (2014) posit that within the proposed timing circuit (cortico-thalamic-basal ganglia) the concurrent encoding of duration and stimulus

attributes in working memory is carried out by mechanisms which respond to distinct spatiotemporal profiles.

One of the theoretical predictions which has been put forward is that the model (like SET) is able to time multiple intervals in parallel. Several past studies have likewise appeared to support this notion (Rule & Curtis, 1985; Brown & West, 1990; Ivry & Richardson 2002). On the basis of a conducted experiment which entails the timing of overlapping intervals, Van Rijn and Taatgen (2008) suggest that a single time source strategically allocates resources which allows for the timing of multiple intervals. This is accomplished by the 'clock' dividing the overlapping intervals into smaller parts, independently estimating them, and then adding them up to obtain the separate interval durations. Upon the appearance of a visual cue, participants were required to reproduce two partially overlapping time intervals, and it was found that the second estimate was highly influenced by stimulus onset asynchrony. The later the second cue appeared the longer was its presumed duration. All three experiments report a positive effect on stimulus onset asynchrony size and duration estimates, which is noted to conform to model predictions and a logarithmic representation of time (Van Rijn & Taatgen, 2008).

1.4.3. Striatal Beat Frequency Model (SBF)

The striatal beat frequency model proposed by Matell and Meck (2004), maintains the so-called clock stage via the coincidental activation of striatal medium spiny neurons by cortical neural oscillators. The onset of an interval is regulated by dopaminergic inputs from the ventral tegmental area which results in the phases of the multiple oscillators being reset (Gu, Rijn & Meck, 2015). Cortico-striatal synaptic weights are a representation of durations already held in memory and the striatum. These weights determine which durations are encoded. Phasic dopamine input to the striatum from the

substantia nigra pars compacta, strengthens the medium spiny neuron synapses with inputs from the oscillating neurons when rewards are received, allowing them to serve as 'detectors' for particular durations (Ullsperger, Danielmeier, Jocham, 2014). The decision stage is accomplished by post-synaptic potentials, and when the firing threshold is reached it is assumed that adequate coincident cortical activity has taken place. The model stipulates that each cortical neuron oscillates at a specific frequency, with many frequencies represented in the complete population. Although these neurons cannot encode all possible times individually, many additional times, including very long durations, can be represented by the unique coincident activation of several neurons at once. The strength of the model is its ability to reconcile some noted behavioural data together with possible neural and pharmacological mechanisms (Allman & Meck, 2012; Coull, Cheng & Meck, 2011; Merchant, Pérez, Zarco & Gámez, 2013).

As noted above, the onset of timing is initiated by the phase-resetting of cortical oscillators by dopaminergic inputs from the ventral tegmental area. A recent animal study (Parker, Chen, Kingyon, Cavanagh & Narayanan, 2014) found that the onset of interval timing was accompanied by a significant burst of power in the theta band (4Hz) in the medial frontal cortex. This could be comparable to the predictions made by the Striatal Beat Frequency model in regards to the reset of neuronal assemblies at the start of a to-be-timed interval. Furthermore a focal disruption of dopamine receptors (D1) in the medial frontal cortex caused by the administration of a selective dopamine receptor antagonist (SCH23390) caused the prominent burst noted above to be much weaker and was behaviourally accompanied by timing deficits in the animals. In another recent study, Mello, Soares and Patton (2015) recorded the spiking activity of striatal neurons in rats, whilst the animals were engaged in an interval timing task. They found that the neural firing corresponded to an interaction between the temporal interval and the rats' sensorimotor state. When the temporal intervals were changed (ranging from 12s to 60s),

the neuronal response was rescaled, suggesting that relative time is being encoded by striatal populations. When striatal function was disrupted by the administration of muscimol (GABBAa agonist) the animals exhibited timing deficits emphasising the significance of normal striatal functioning in temporal processing.

Other studies have not provided clear-cut support as is the case with an experiment conducted by Wiener, Turkeltaub and Coslett (2010) who using activation likelihood estimation, found that although clusters of activation likelihood in the basal ganglia and regions of the cortex during sub-second motor timing were noted, this effect did not extend to supra-second tasks. Similarly a lesion study conducted with two subjects suffering from bilateral lesions of the basal ganglia, found no significant deficits in time estimation, production or reproduction. However, both participants were severely impaired in a rhythmic tapping task indicating that the basal ganglia may be crucial to particular motor timing functions (Coslett, Wiener & Chatterjee, 2010).

1.4.4. Inhibitory oscillation (EIO) model of temporal processing

The coupled excitatory – inhibitory oscillation model (EIO; Gu et al, 2015) is an extension of the SBF model. The focus is on the noted underlying neural oscillations described in the SBF model. Dual oscillator components, namely excitatory and inhibitory inputs to each neuron, are detailed and expanded to neural populations to provide an integrative model of interval timing and working memory. The EIO model has a basic similarity to a model of place and grid cell firing and theta rhythmicity (Burgess & O'Keeffe, 2007; Burgess & O'Keeffe, 2011). Although the EIO model substitutes the baseline inhibitory oscillation at the frequency of local field potentials with inhibitory oscillation which represents population feedback. The frequency of excitatory oscillations is assumed to vary between neurons and is suggested to be an influential factor in the

encoding of interval durations. Behavioural variability in timing could be explained through variations in the oscillation speeds of individual neurons modulated by dopamine input, an update to the SBF model which posited that the entire network would be subject to either slowing or speeding up. A dissociation of sub- and supra-second timing whereby different frequency ranges contribute to different time scales is also proposed, linking the processing of longer intervals to theta and delta oscillations. Specific target durations are said to stem from an interactive process of timing and working memory which arises from the same neural representations. The authors state that this integrated model possesses the framework detailed by the Scalar Expectancy Theory model. Traditionally noted components such as a stand-alone accumulator and pacemaker are not required in EIO due to the interaction with other cognitive processes and memory in particular, because as in the ACT-R model, timing is regarded as a component of a larger cognitive architecture.

1.5 Partitions in Timing.

An examination of different timing behaviours and durations can serve to better reveal the underlying temporal substrates. The following sections look at evidence pertaining to dissociations in timing and the implications thereof.

1.5.1. Sub- and supra-second timing

Intervals of varying durations are associated with different behaviours, for instance the production and estimation of sub-second intervals is imperative to language (e.g. Diehl, Lotto, & Holt, 2004) and motor control (e.g. Hore, Wild & Diener, 1991; Merchant & Georgopoulos, 2006) - these behaviours are said to rely on automatic processing. Supra-second durations relate to what could be termed as conscious time estimation, involved in

decision making and probably relying on other cognitive processes such as attention and memory. Dissociations in the processing of different time scales using a variety of paradigms have been noted in the timing literature.

Pharmacological studies have provided strong evidence to suggest the involvement of distinct mechanisms in sub- and supra-second timing. The role of dopamine, now relatively well established in temporal processing, has revealed its selective involvement in sub- and supra-second timing. When haloperidol (a dopamine receptor antagonist) and midazolam (a benzodiazepine, acting on GABAa receptors) are administered, interval discrimination in the 1s range is impaired although duration discrimination in the 50ms range is only affected by haloperidol (Meck, 1996). The deficiency caused by midazolam is believed to stem from its interference in working memory. Remoxipride (an antipsychotic, with a specific mechanism of action on D2 dopamine receptors) has likewise been noted to impair timing in the supra-second range whilst leaving sub-second timing unaffected (Rammsayer, 1997, 1999).

Although overlapping activation of various brain regions has been noted in neuroimaging studies, there are nonetheless differences in activation during investigations between sub- and supra-second timing (Lewis & Miall, 2003a; Macar, et al. 2002; Pouthas et al. 2005; Matell, Meck & Nicolelis, 2003). Subcortical structures such as the cerebellum and basal ganglia have most often been noted to mediate temporal processing in the range of tens to hundreds of milliseconds (Lewis & Miall, 2003; Mauk & Buonomano, 2004; Wiener, Turkeltaub and Coslett, 2010), whilst timing of intervals in the range of seconds-to-minutes has often been attributed to brain regions also involved in working memory such as the dorsolateral prefrontal cortex (Jones, Rosenkranz, Rothwell & Jahanshahi, 2004; Lewis & Miall, 2003a) and Supplementary Motor Area. (Macar et al, 2002; Ferrandez, Hugueville, Lehéricy, Poline, Marsault & Pouthas, 2003).

A study by Wiener, Lohoff and Coslett, (2011) looked at gene polymorphisms which modulate dopaminergic activity in relation to the timing of supra- and sub-second intervals. The first, COMT Val158Met is associated with an increased activity of the COMT enzyme which degrades dopamine such that catabolism of synaptic dopamine is greater in the pre frontal cortex. It has been suggested that the timing of supra-second intervals is linked to dopamine transmission in the dorsal frontostriatal circuit (Jones et al, 2004; Matell & Meck, 2004). COMT inhibitors on the other hand, are used in Parkinson's disease treatment, their function to spare levodopa from the COMT enzyme and prolong its activation (Dutta & Weidon, 2006). The second gene polymorphism − DRD2/ANKK1-Taq1a is associated with reduced striatal D2 receptor binding (Savitz et al, 2013). D2 receptors are the main mediators of known dopamine functions, and presumably, due to the involvement of the neurotransmitter, in interval timing. An increased activity of D2 receptors has been noted to interfere with normal cognitive functioning including working memory (Kellendonk, Simpson, Polan, Malleret, Vronskaya, Winiger, Moore & Kandel, 2006). Transgenic mice which selectively overexpress D2 in the striatum have also been noted to display distinct timing deficits (Drew, Simpson, Kellendonk, Herzberg, Lipatova, Fairhurst, Kandel, Malapani & Balsam, 2007). Similarly abnormalities in the D2 receptor structure and increased receptor densities have been implicated in neurological disorders (Seeman, & Niznik, 1990) which exhibit timing deficits such as schizophrenia and Parkinson's disease (e.g. Ward, Kellendonk, Simpson, Lipatova, Drew, Fairhurst, Kandel, Moore & Balsam, 2009)

Wiener et al. looked at the point of subjective equality (PSE), difference limen (DL; upper or lower threshold) and coefficient of variation (CV) for each of several durations in a temporal discrimination task and the results were compared to the genetic status of participants. It was noted that subjects with the DRD2/ANKK1- Taq1a polymorphism

exhibited an increased CV during temporal discrimination of sub-second intervals. The DRD2/ANKK1- Taq1a polymorphism is noted by the authors to have an effect mainly restricted to the basal ganglia whilst those with the COMT Val158Met polymorphism, had an increased CV in the supra-second duration range. The authors propose that these results shed light on the potential genetic basis for the previously suggested dissociation in the timing of sub- and supra-second intervals.

The timing of longer durations is associated with cognitive components, such as memory and attention, and so it could be assumed that any effects of temporal training would be more pronounced in supra-second intervals. Brandler and Rammsayer (1994) assigned participants to auditory interval discrimination training in either a sub- or supra-second group. They found that training improved performance in longer durations and as hypothesised, no significant effect was noted in very brief durations. The authors suggest that their results support the notion of duration-specific timing mechanisms. Lewis and Miall (2009), investigated a wide range of durations (68msec to 16.7min) in an attempt to locate the 'break point' between sub- and supra-second timing. They looked for changes in CV in a reproduction study, based on the premise that that would reflect a switch between duration specific timing mechanisms. No 'break points' were found, instead a gradual trend whereby increased duration corresponded to a decreased CV was noted. The authors suggest that this could be an indicator of a single clock, but equally it could also point to an overlapping of distinct mechanisms with similar CV's.

1.5.2. Perceptual and motor timing

Timing is imperative to both perception and action but as yet it is not entirely clear whether these processes share a common underlying mechanism. Human experience often includes the need for an interaction of both forms of timing; ranging from simple activities such as crossing the street or catching a falling object, to playing an instrument.

Hence, intuitively it seems likely that at least a partially overlapping system may be utilised.

Behavioural studies investigating motor and perceptual timing have often relied on a comparison of the obtained variance in an attempt to reveal possible dissociations between these two forms of timing. Building on an earlier correlational study (Keele, Pokorny, Corcos & Ivry, 1985) which found a significant albeit moderate correlation (.52) between tasks employing motor and perceptual timing, Ivry and Hazelltine (1995) used slope analysis (so as to eliminate duration-independent sources of variance), to further investigate variability in motor and perceptual tasks. The basic principle of slope analysis posits that timing variance obtained during a task comprises of variance which can be attributed to duration (i.e. which increases as the interval increases) as well as duration-independent variance which remains constant (Ivry & Hazeltine, 1995). If the slope of the variability functions of the two tasks is comparable, a common timing mechanism can be presumed. In their first experiment they found the slope for the production task to be less than that of the perception task, which could suggest the involvement of distinct mechanisms. The authors suggested that that this result was more likely to stem from different task demands and so by adjusting the presentation of target intervals in their second experiment, they obtained very similar slope values for both the perception and production tasks. Memory for distinct interval durations in motor and perceptual timing has been noted to vary (Bueti & Walsh, 2008), although the most significant differences were noted at the shortest (300ms) and at the longest (1200ms) durations. Additionally the contribution of memory to perceptual timing may be a more significant component than in the case of motor timing which is believed to rely on more 'automatic' processes (Lewis & Miall, 2003b).

Different neuroimaging studies have at times provided disparate results. This could partially be due to the utilised methodology, limited to not only the nature of the task, but also to the length of the investigated intervals. Motor timing usually relies on durations in the sub-second range, and so it is conceivable that a subset of the noted dissociations could be due to the interval range rather than dissociations based on the type of timing (i.e. action & perception). Nonetheless, studies using the same durations and relatively well-matched tasks have found some differences in activation. Bueti, Walsh, Frith and Rees (2008) found distributed activation over several cortical and subcortical regions, with a common activation of the cerebellum and basal ganglia when participants were engaged in a series of motor timing and visual estimation tasks. Behavioural differences, whereby a delayed response bias of up to 8s was observed in the reproduction task were not seen in the interval estimation task. Significant differences in neural activation were noted during the two tasks with a wider cortical region involved during the reproduction task. Particular attention was given to the differential activation of the inferior parietal cortex (IPC) during the tasks, a neural region previously noted to be involved in timing (Lewis & Miall, 2003a, 2003b; Rao, Mayer, & Harrington 2001). The parietal cortex integrates sensory information from different modalities (Caspers, Geyer, Schleicher, Mohlberg, Amunts & Zill, 2006) and Bueti et al. suggest that the parietal cortex also serves as an interface for motor and sensory processes. The authors suggest that distinct timing mechanisms underlie motor and perceptual timing and the parietal cortex allows for their interface.

Schubotz, Friederici and Cramon, (2000) used an oddball paradigm in their study, a sustained presentation of auditory intervals and visual patterns which ‘moved’ at particular rates over successive frames in order to create a rhythm. These tasks were used to ascertain as to whether the neural regions which are involved in the preparation of movement are also used in the perception of time. Based on the noted activation in

similar neural regions for both of the tasks (supplementary motor area, the lateral premotor cortex, the frontal operculum the anterior and the posterior intraparietal sulcus, basal ganglia) the authors suggest a common mechanism for motor and perceptual timing.

Linking motor timing to sub-second durations and perceptual timing with supra-second durations could possibly explain some of the discrepancies noted in studies looking at dissociations between the two forms of timing. As pointed out by Lewis and Miall (2003a) who provided a broad review of neuroimaging studies, movements generally occur in a time frame associated with a much shorter duration i.e. a range of sub-seconds, and so they divided the considered studies on the basis of 'automatic' and 'cognitively controlled' timing. They note that in studies involving the former, activation is noted in the bilateral supplementary motor area, sensorimotor cortex, the cerebellum, the lateral premotor area, the right superior temporal gyrus as well as the basal ganglia. The latter on the other hand shows high activity in the dorsolateral prefrontal cortex as well as the prefrontal and parietal cortices, regions associated with memory and attention. Nonetheless, a number of regions are noted to overlap with varying degrees of activation

1.5.3. Timing across different modalities

Our experience of time, or as described by timing models; clock speed, is affected by a variety of different factors; temporal context, attention, memory, emotions and bodily states are some of the most prominent (Effron, Niedenthal, Gil, Droit-Volet, 2006; Hicks, Miller, Gaes, Bierman, 1977; Jazayeri & Shadlen, 2010; Macar, Grondin, Casini, 1994; Meck & Lake, 1983; Meissner & Wittmann, 2011; Van Rijn & Meck, 2015; Droit-Volet & Meck, 2007; Wearden, O'Donoghue, Ogden & Montgomery, 2014) Subjective time has also been noted to vary with modality (e.g. Goldstone & Lhamon, 1974, Allen, 1979; Church, 1984; Wearden, Edwards, Fakhri & Percival, 1998; Wearden, Todd, & Jones,

2006). Modality specific stimulus features such as frequency (Kanai, Paffen, Hogendoorn, & Verstraten, 2006) numerical value (Xuan, Zhan, He & Chen, 2007) and eye movements (Yarrow, Haggard, Heal, Brown & Rothwell, 2001) have been noted to affect the perceived duration of an interval, and could be an indicator of modality specific timing mechanisms. Auditory intervals are estimated as longer than visual intervals of the same duration (Wearden, Edwards, Fakhri & Percival, 1998; Penney, Gibbon & Meck, 2000; Droit-Volet, Tourret & Wearden, 2004). Wearden et al. also found modality differences increased with longer durations. The authors propose two interpretations of the observed disparity in the context of the internal clock model, and suggest that the combined effect of the two sources of variability is able to account for their results. Pulses are generated at a constant rate and the slower the pacemaker rate, the higher the resulting variability (Gibbon, 1977). This would account for the obtained results and the slower pacemaker speeds associated with visual stimuli but, previous studies suggest that although pacemaker speed is a contributing factor it is not a major source of variability (e.g. Gibbon, Church & Meck, 1984). It is also considered that the variability may be due to a more variable onset and offset switch particular to the visual field – this would affect the accumulation of pulses and therefore the experienced duration.

Studies have shown that preceding stimuli with a train of clicks alters the perceived duration (e.g. Penton-Voak, Edwards, Percival, & Wearden, 1996; Treisman, Faulkner, Naish, & Brogan, 1990). This method was employed by Wearden et al. who likewise observed the effect in both vision and audition. Differences in variability between modalities remained even when the subjective length was changed, suggesting that variability stemming from the switch component was an additive source to pacemaker derived variability (subjective length difference). By using an equation for pulse accumulation, a between-modality effect of different switch opening and closing latencies was seen in one of the experiments but not the other. The similarities described by the

data, whereby both modalities adjust rates in a similar manner in response to stimuli noted to manipulate the subjective perception of length, are said to provide evidence for a common pacemaker accumulator system.

The role of short-term memory and decay rates in a series of timing tasks was similarly noted to show an advantage in the auditory domain, although this was found specific to sub-second durations (Collier & Logan, 2000). Not all studies have shared these results though, Grondin (2005), who looked at the extent to which memory contributes to timing variance, found no difference in the perceived duration of a time interval between modalities. Grondin states that the results of his study – variance increased with memory demands and no modality effect – is in accordance with the SET model of timing.

Timing studies have used training to investigate transference of learning across modalities and durations (e.g. Karmarkar & Buonomano, 2003; Bartolo & Merchant, 2009; Grondin & Ulrich, 2011). Performance improvements in perceptual discrimination tasks have been observed to translate to frequencies and durations matching the trained, but not the untrained frequencies and durations (Wright, Buonomano, Mahncke & Merzenich, 1997). Meegan, Aslin & Jacobs (2000), trained two groups of participants on an auditory interval discrimination task, for the first group the shorter standard interval was always 300ms, and 500ms for the second group. Two experimental motor tasks, only one of which contained the learned interval duration, were then completed. Motor timing improvements were found to be specific only to trained auditory durations. A similar study, trained participants on an interval production task together with a somatosensory temporal generalisation task (Planetta & Servos 2008), in either a 500ms or 800ms groups (as above). As with the above described findings, the results of this study note a reduction in timing variability, extending to untrained tasks and modality but specific to duration.

Auditory interval discrimination training was found to improve performance in tasks with filled intervals of the same duration and frequency as the practised empty intervals, but no cross-modal effect from audition to vision was observed (Lapid, Ulrich & Rammsayer, 2009). Bratzke, Seifried and Ulrich (2012) investigated cross-modal transfer in sub-second timing in vision and audition. Participants in the two experimental groups completed training over four days in either auditory or visual interval discrimination. Auditory training was found to improve performance in the visual task but the effect was not observed in the other direction – from vision to audition. The noted transfer of learning between modalities was also found to be duration specific. Implicit timing tests (Ternus test; see Chen, Shi & Muller, 2010) have also been used to test participants' timing performance pre- and post- cross-modal training (Chen & Zhou, 2014). A between-group design was employed and participants were allocated to auditory, visual or spatial interval discrimination training before taking part in one of the seven experiments. The initial analysis revealed no significant main result of test or experiment in the *point of subjective equality* and a main effect of test in the *just noticeable difference*. The effects were then tested separately for each experiment. Explicit auditory and spatial, but not visual training, was noted to improve cross-modal post-test performance in the sub-second range.

Overall, evidence relating to timing across different modalities is mixed, likewise the case for cross-modal transfer is not fully supported, but the findings do generally point to duration-specific timing mechanisms. Based on the current studies it appears that timing is not mediated by a single supramodal temporal mechanism, although an overlap of neural regions is very much conceivable.

1.5.4. Implicit and Explicit Timing

As discussed above, a number of partitions in timing have been proposed, but of particular note is the disparity between explicit and implicit timing. Whilst explicit timing relies on an overt measure of duration, implicit timing is the result of a non-temporal task, for which time is nonetheless an essential component. A commonly used method of investigation in implicit timing requires the participant to respond once a stimulus has reached its target, as is the case in collision judgements whereby the speed and the predicted location of the travelling stimulus requires accurate temporal processing despite not being the task focus. It is also important to note that the distinction refers to the underlying processes rather than simply the task requirements.

Studies seeking to elucidate whether explicit and implicit timing depend on the same temporal representation have utilised a variety of methods. A common approach in psychophysical research looks at correlations in performance (assessed as timing variability) between tasks, with a high correlation likely to indicate a common timing process. For example, continuous circle drawing and repetitive finger tapping tasks have respectively been categorised as relying on implicit and explicit timing (Zelaznik, Spencer & Ivry, 2002). No correlations between timing variability across individuals in the two motor tasks have been noted (Robertson, Zelaznik, Lantero, Gadacz, Spencer & Doffin, 1999; Zelaznik, Spencer & Doffin, 2000). Spencer and Zelaznik (2003) employed slope analyses in the circle drawing and finger tapping tasks and report significant distinctions in the underlying timing processes between the two temporal representations, suggesting dissociable temporal mechanisms.

The impact of task goals on the internal representation of a duration and the proportional error in estimation was investigated by Piras and Coull (2011).The study analysed the variability of implicit and explicit timing data. A temporal generalisation task was used in

the explicit condition and a temporal expectancy task in the implicit condition – a warning cue, followed by an interval from a set range of durations would alert participants to prepare for action and respond as soon as the target was spotted. Both explicit and implicit timing was observed to conform to scalar law, and a uniform linear relationship between subjective and real time was described. Although the authors suggest that perceptual timing in explicit and implicit tasks share the same temporal representations, the variance increment with increasing durations was noted to vary. For durations ranging from 600ms to 1400ms, variability in the implicit task was noted to be significantly larger despite comparable implicit/explicit estimates in the 200ms range. These findings suggest a possible functional separation between the two forms of timing.

Multidimensional scaling, noted to reflect the vital elements of a dataset by reducing the number of dimensions and displaying measures of similarity between variables (Shepard 1980), was utilised by Merchant, Zarco, Bartolo and Prado (2008) to investigate the mechanisms of implicit and explicit timing. A battery of tasks all based on an equivalent temporal range (350ms to 1000ms) including both motor and perceptual tasks showed a significant dissociation between explicit and implicit timing. Cerebellar lesion studies have shown a similar distinction using corresponding motor tasks; Continuous circle drawing was noted to remain unaffected but deficits in interval production were observed (Spencer, Zelaznik, Diedrichsen & Ivry, 2003; Koch, Olivieri, Torriero, Salerno, Lo Gerfo & Caltagirone, 2006). The circle drawing task instructions in the Merchant et al. study required participants to follow a circular path, 5cm in diameter within a given time interval. Although the authors note that the task instructions emphasised temporal precision, they nonetheless acknowledge that the noted behavioural difference between tasks could be at least partially due to the prominent spatial element in this paradigm rather than simply to implicit timing.

Contingent negative variation waves (event related potentials which are components of the EEG) have been noted to reflect the neural activity during duration estimation and temporal reproduction tasks (Macar Vidal & Casini, 1999; Pfeuty, Ragot & Pouthas, 2003). Correlations between amplitude and duration estimation as well as the latency of CNV termination and duration reproduction have been observed (Ruchkin, McCalley & Glaser, 1977). When comparing the contingent negative variation waves in an implicit choice response task to those from previously conducted explicit timing studies, Praamstra, Kourtis, Kwok & Oostenveld (2006) found comparable temporal properties suggesting the presence of a qualitatively similar mechanism. Praamstra et al. (2006) noted predominant contingent negative variation activations of the left and right premotor cortex in their implicit condition whilst activation of the supplementary motor area or the medial premotor cortex (Macar et al, 1999; Pfeuty, Ragot & Pouthas, 2005, respectively) was observed during explicit tasks.

Neuroimaging studies looking at explicit timing have converged on several key regions including the supplementary motor area, the cerebellum, basal ganglia as well as the right inferior frontal cortices (Schubotz, Friederici, von Cramon, 2000; Ferrandez et al, 2003; Bueti, Walsh, Frith & Rees, 2008; Coull, Nazarian, & Vidal, 2008). Investigations of implicit timing have often revealed activation of the inferior parietal cortex (Assamus, Marshall, Noth, Zilles & Fink, 2005), the cerebellum and the sensorimotor regions of premotor and parietal cortices (Field & Wann, 2005). Substantial variability in brain region activation has been noted in neuroimaging literature and it is expected that some of the described activity is due to non-temporal processes often associated with specific task demands. Nonetheless, a distinction between neural activation can be detected when studies are categorised according to duration, motor demands and task requirements, specifically referring to task predictability and continuity (Lewis & Miall, 2003b). More recent studies, albeit not specific to temporal tasks, propose that distinct neural networks

are involved for over-learned sequences (Pariyadath, Churchill & Eagleman, 2008). Lewis and Miall further developed the task traits to map onto so-called automatic and cognitively controlled timing which complement the above noted findings by Rammsayer (1999) as well as Wiener, Lohoff and Coslett (2011). Likewise as noted by Coull and Nobre (2008) the division is said to loosely converge with the distinction between explicit and implicit timing. Based on a meta-analysis of studies investigating timing dysfunctions in neuropsychiatric disorders and traumatic brain injury, Piras et al. (2014) have proposed a partially overlapping network of neural regions involved in explicit and implicit timing. The impact of contextual demands and the involvement of cognitive components such as memory and attention in the two forms of timing, has additionally been noted to affect the activation of particular brain areas. The processing of temporal information by central timekeeping cortical and subcortical structures (such as the supplementary motor area, prefrontal and posterior parietal cortex, basal ganglia and cerebellum) has been suggested by earlier studies to be mediated by the correspondent processing of context-dependent information in other brain regions (Grondin, 2001; Lewis & Miall, 2003). Furthermore, Piras et al. detail the functional roles of neural regions in explicit timing and suggest that implicit timing or temporal expectation involves the left premotor-cerebellar-parietal circuit which receives updates from the right prefrontal cortex in regards to the expected delay. The estimated duration is then encoded by the supplementary motor area and the superior temporal cortex to aid future predictions.

1.6. Implicit Timing: Language

Language relies on implicit timing; it is bound by a stringent temporal structure, and our ability to understand speech, and the correct linguistic context, often depends on precise temporal cues. Prosodic information which to a large extent depends on pitch, has been noted to involve a strong timing component (Moore & Glasberg, 1986; Rosen & Fourcin,

1986). A study modelling the perception of a concurrent presentation of vowels with different frequencies found that performance by participants could only be accounted for, if temporal features were included (Assmann & Summerfield 1990). Timing and speech are closely intertwined; several lines of research propose that a variety of language disorders at least partially stem from temporal disturbances (Olander, Smith & Zelaznik, 2010; Sidiropoulos, Ackermann, Wannke & Hetrich, 2010; Steinbrink, Groth, Lachmann & Riecker, 2011). Similarly studies attempting to differentiate between task demands and timing have found temporal processing to be closely linked to the pre-supplementary motor area and supplementary motor area -proper (Macar, Anton, Bonnet & Vidal, 2004; Coull, 2004). It is therefore likely that timing in language relies on mechanisms which could be related to other forms of implicit perceptual and motor timing.

Although it was initially thought that accurate speech recognition requires spectral information, studies have shown that even when the majority of spectral information is replaced with noise, comprehension is relatively unaffected due to the maintenance of temporal information (Shannon, Zeng, Kamath, Wygonski & Ekelid, 1995). The neural substrates of timing in speech processing were investigated by Geiser, Zaehle, Jancke and Meyer (2008) who propose a strict hemispheric lateralisation between implicit and explicit timing in language. Focusing on speech rhythm, an essential element of spoken language, noted to aid accurate word perception (Friedrich, Kotz, Friederici & Gunter, 2004) the study investigated neural activation in the two conditions. Participants in the explicit group were required to judge whether a given sentence was isochronous whilst participants in the implicit group, using the same stimuli, were advised to focus on prosody and deem whether the presented sentence was a question or statement. The stimulus material consisted of German pseudo sentences. German, similarly to English, is a stress-timed language whereby a timely allocation of accented syllables makes up the speech rhythm. Isochronous sentence processing in the explicit group in the Geiser et al.

study, revealed activation in the right superior temporal gyrus whilst the supramarginal gyrus and the superior temporal gyrus were noted in the implicit group. Likewise, task performance was closely linked with the activation of mesial premotor cortex (pre-supplementary motor area and supplementary motor area-proper) noted predominantly in the right hemisphere in the explicit group. Activation of the pre- supplementary motor area in particular, has been proposed to specifically reflect processes involved in temporal discrimination (Pastor, Macaluso, Friston, Day & Frackowiak, 2004).

Speech is organised on a number of timescales and the differentiation of speech sounds such as phonemes for example, ranges from tens to hundreds of milliseconds. A recent neuroimaging study (Overath, McDermott, Zarate & Poeppel, 2015) utilised these timescales in order to create sound segments of different durations, which they termed 'quilts', in order to analyse the temporal elements involved in speech. So as to eliminate any confounding effects, the 'quilts' were created in German, a language foreign to the participants but at the same time one which preserved certain phonological aspects in order to employ speech appropriate mechanisms ('quilts' derived from environmental sounds were utilised in the control condition). The superior temporal sulcus showed strong activation, a region previously associated with speech perception (Redcay, 2008). Overath et al. found significant variations based on segment length indicating a sensitivity to temporal components irrespective of lexical, semantic or syntactic processes. Parametric sensitivity was noted to increase with duration up to a point, a plateau was reached at approximately 500ms. The authors suggest that the superior temporal sulcus may be involved in an analysis of speech structures such as phonemes and syllables, whilst linguistic processing requiring longer durations and aiding comprehension is facilitated and integrated in other neural regions, such as the superior and medial temporal gyrus. If the timing mechanisms which are involved in language processes are related to other forms of timing, a speculative suggestion would be that the

noted plateau in the study is a reflection of the dichotomy observed between sub- and supra-second timing as observed in other forms of motor and perceptual timing.

1.7. Aims and overview

What is the fundamental mechanism underlying human timing? Psychophysical methods have revealed certain characteristics pertaining to the timing of short durations, and so deviations from the suggested fundamental properties are descriptive of the mechanisms of interval timing. Weber's Law has been noted to hold for an interval range of at least 0.2 to 2sec (for review see Grondin, 2001). In Chapter 3 I will investigate this property in detail. This is important, because many clock models are designed to explain scalar timing or particular deviations from it. However, the scalar property is not the only source of variance in timing tasks; additional noise irrespective of the timed duration is a pervasive component. In accordance with the internal clock model, variance can be assumed to arise in each of the clock components and so discriminating between two intervals will include a certain amount of non-scalar variance. Under some models, modifying a classic interval comparison task so that the participants are required to compare the duration of one interval to a 'broken' one would require an additional closing and opening of the switch as timing is paused and restarted (introducing only non-scalar noise). The stopwatch and ACT-R models will be examined in light of these predictions in the first experimental chapter (Chapter 2).

A second key question in timing research pertains to the underlying architecture, or as otherwise put – one clock or many? Dedicated models propose that timing is accomplished by a centralised supramodal mechanism, which includes motor and perceptual timing across different durations, whilst intrinsic models have a distributed design, with different timing behaviours relying on specific neural circuits (Mauk &

Buonomano, 2004; Ivry & Schlerf, 2008). Psychophysical studies have alluded to a central clock although neuroimaging studies have not been able to pinpoint such a dedicated neural region. Distributed activation, albeit with a frequent overlap in brain regions, is nonetheless often observed (e.g. Lewis & Miall, 2003b; Wencil, Coslett, Aguirre & Chatterjee, 2010). As outlined in the preceding sections, two behavioural approaches to investigate this issue are transfer of training and correlation. I make use of these methods in Chapters 4 and 5 respectively. These experiments aim to investigate explicit and implicit timing, both in the motor and perceptual domain, with particular attention bestowed upon language. The level of temporal precision and accuracy (bias) is compared across tasks and correlation analysis conducted, based on the premise that if the same temporal mechanism is employed in the varying tasks, performance should be significantly correlated. A final experiment investigates whether any transfer of learning effects are present after intense training and whether these translate across modality and durations.

CHAPTER 2 – HUMANS DON'T TIME SUB-SECOND INTERVALS LIKE A STOPWATCH

Note – the experiment described in this chapter was published as part of the following article:

Narkiewicz, M., Lambrechts, A., Eichelbaum, F. & Yarrow, K. Humans don't time sub-second intervals like a stopwatch. *Journal of Experimental Psychology: Human Perception & Performance,* 41, 249-263 (2015).

Because the work described here formed the final part of the article, this chapter is an edited version of that presentation. The earlier experiments from the article, representing work by other students prior to the initiation of this PhD, are referred to herein simply as "pilot work conducted in the Yarrow lab."

INTRODUCTION

Interval timing underpins a wide range of sensory, cognitive, and motor behaviours, so it is not surprising that humans and other animals are able to attain relatively accurate and precise timing in the milliseconds to minutes range (Allan, 1979; Grondin, 2001). Many models have been proposed to illustrate and explain timing performance, suggesting various metaphors for the timing process. These range from binary oscillators to plastic neural networks (Matell & Meck, 2004). However, the most pervasive metaphor is that of the stopwatch.

In their most basic form, such counter models (Creelman, 1962; Treisman, 1963) posit a pacemaker that generates a series of pulses that measure out roughly equal units of time. These are integrated, for example, by being sent to an accumulator and stored, while a "switch" is closed, but are no longer accumulated when the switch is open. The switch itself would typically be closed only during an interval of interest that is being timed. The collected pulses then correspond to the amount of time that has passed, so that when an

interval comparison is required, the accumulated pulses can be compared with a stored value representing a specific duration. Despite the rise of alternate timing models in recent years (for reviews see, e.g., Buhusi & Meck, 2005; Ivry & Schlerf, 2008), the counter model remains prominent in the field of temporal research, most likely due to its conceptual simplicity, and also its flexibility, which allows it to explain a wide range of timing behaviours.

An established method in prospective timing research involves discriminating between two different intervals—a standard, which either remains constant throughout the experiment or "roves" between a small number of base durations, and a target interval, which varies from trial to trial, straddling the standard/s (Grondin, 2001). Counter models are well able to predict behaviour in this task. In this study, the target interval was split into two parts, and participants were required to combine these durations and then compare their sum to the standard. Similar experiments, albeit with longer intervals and somewhat different tasks, have been conducted in both animals and humans (e.g.,Buhusi, Sasaki, & Meck, 2002; Buhusi & Meck, 2006; Fortin & Massé, 2000) although the use of longer intervals would allow for counting strategies (in humans), which is an issue avoided in the present experiment by using sub-second intervals.[1]

It is assumed that this "pause" feature is implicit in most counter models. Indeed, theorists have previously argued that this is possible using the SET framework (e.g., Lejeune, 1998; Roberts & Church, 1978), and have used such a pause/restart process to explain success on split-interval tasks in humans and animals. For example, Fortin and Massé (2000) had participants reproduce a target duration after hearing an interval containing a break, and participants were found to reproduce intervals fairly accurately. The fact that participants were successfully taking account of the breaks seems to support

1 Note that although some counter models were not initially intended to deal with short intervals, counter models have often been posited to account for experimental results with stimuli as short as 100 ms (e.g., Getty, 1975; Rammsayer & Ulrich, 2005; Wearden et al., 1998).

the idea of a counter-based clock that can be paused, and was interpreted in this context (although this was not the main subject of investigation). Furthermore, these authors and their collaborators have subsequently shown that accurate timing can be obtained from humans with broken intervals in several tasks, not just reproduction (Fortin & Tremblay, 2006; Fortin, Fairhurst, Malapani, Morin, Towey, & Meck, 2009; Tremblay & Fortin, 2003). In a similar vein, animal work suggesting success at pausing the timer during gaps in the peak-interval procedure (e.g., Roberts & Church, 1978; see discussion for further details) appears to have partly motivated the original inclusion of the switch within the SET framework (Buhusi & Meck, 2000).

In temporal psychophysics, it is standard practice to parcel up trial-by-trial errors into bias, or constant error, which reflects mean accuracy over multiple trials, and variable error (or its inverse, precision), which reflects the extent of trial-by-trial deviation from the average. The apparent successes at pausing and restarting accumulation described above stem from analyses focusing on accuracy. Here, instead the focus is on predictions about precision, such that the logic presented below has not, to our knowledge, been expounded or tested before.

Pilot work conducted in the Yarrow lab focused on Scalar Expectancy Theory (SET). Within this particular counter model all that would be required when timing a broken target interval (compared with an unbroken one) is an additional opening and closing of the switch (to halt accumulation during the break). This operation was assumed to add a certain amount of nonscalar noise to the task, i.e. a noise component that arises irrespective of stimulus magnitude.

The maximum variance associated with the additional opening and closing of the switch was calculated using the generalized version of Weber's law. The standard deviation of

variable errors increases linearly with interval duration, which means that total variance follows a power function:

$$\sigma^2 \text{ observed} = st^2 + c \quad (2.1)$$

Where t is the standard interval's duration, s is the scalar variance, and c is the constant (nonscalar) variance. An estimate of s and c can then be obtained by assessing performance at two or more standard intervals and extrapolating the function that joins these points through a notional interval duration of zero.

In the classic interval comparison task, the switch will be opened and closed an equal number of times irrespective of interval duration, and therefore the variance associated with these two switch operations (σ^2 switch) is nonscalar and included in c:

$$\sigma 2 \text{ switch} \leq c \quad (2.2)$$

Although two different participant strategies in response to the task were considered, the one which gives stopwatch models more leeway for success was employed. In this version participants were assumed to form an internalized standard (based on earlier trials from the experiment) and thus they did not have to rely on a new estimate for the standard interval on every trial, For the classic task, only one close and open operation would generally be carried out per trial (for the target interval), so σ^2 switch is then an estimate of just one switch operation:

$$\sigma 2 \text{ switch} = \sigma 2 \text{ close\&open} \quad (2.3)$$

The broken-interval task would require the single switch operation from the classic task, together with an additional switch operation for the second segment of the (broken) target

interval. Consequently, performance was posited to not deteriorate in the split-interval task by more than c compared with the standard interval comparison task:

$$\sigma 2 \text{ Increase} \leq c \tag{2.4}$$

Two experiments were conducted, assessing how much performance deteriorated in the split-interval task to test constant-rate pacemaker models like SET at short intervals. The second experiment allowed additional practice (of 120 trials) as well as feedback in order to make this practice as effective as possible. The findings from both these experiments provided evidence that performance on interval comparison tasks deteriorates sharply when the target is broken up so that the putative internal stopwatch must be paused and restarted. The result makes it unlikely that the SET model, as currently specified, can fully account for human timing in the sub-second range.

The present experiment went on to examine the more complex predictions derived from a modified counter module, proposed by Taatgen, van Rijn, & Anderson (2007). This variant embeds a stopwatch timing component within the broad-ranging "adaptive control of thought—rational" (ACT–R) architecture. Although the authors did not conceive their work to be applicable to sub-second intervals (H. Van Rijn, personal communication), the timer they propose might reasonably be adopted by others as a suitable mechanism to explain the pattern of data in the above mentioned experiments. The critical feature of this variant is that in place of a pacemaker with an (on average) constant tick rate, the authors propose a tick rate that slows over time. This proposal has the attractive property of generating scalar variance without the rather arbitrary seeming multiplicative noise that has been incorporated into SET (a feature for which SET has been explicitly criticized; Staddon & Higa, 2006), although it still requires a noise term that is proportional to the inter-tick interval. If pacemaker rate declines across a timed interval, clear predictions

emerge about what should happen to an observer's precision if the interval is split into two or more parts. If we assume that tick rate is reset when the clock is merely paused, the granularity of time will be returned to its initial high acuity state for the second part of the interval, so resolution/precision will actually improve (relative to the typical comparison task without any split), although accuracy will be worse. As this prediction about precision was clearly violated in the above discussed experiments, it was not further considered in the present study. Similarly, if we assume that click rate is somehow maintained through the break and then begins to decline again, the prediction becomes identical to that of the constant rate clock that has already been found wanting. However, if we assume that tick rate is not reset unless a new interval estimate is required, and thus that the pacemaker continues to slow during the break in split-interval conditions, we can predict that temporal resolution will be lower in the second part of a split-target interval compared with the equivalent segment of a whole interval (Figure 2.1)

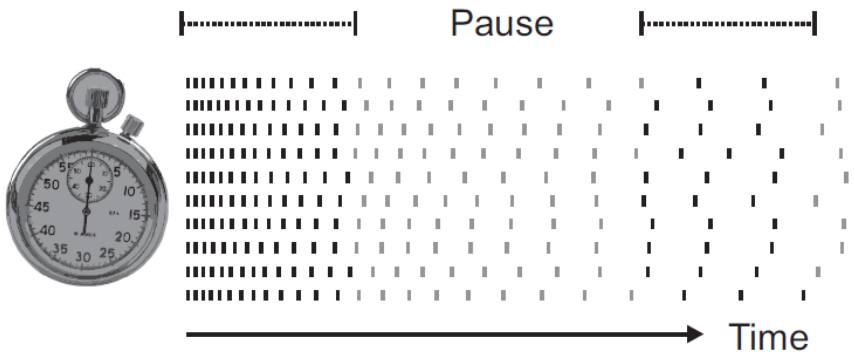

Figure 2.1. Figure 4. Schematic illustration of an internal stopwatch with a slowing pacemaker (Taatgen et al., 2007). Timing of a split interval is shown (300/500/300 ms for the first segment/break/second segment, respectively) above 10 simulated trials. The ticks that would be accumulated are shown in black, and those that would fall in the gap are shown in grey. The second half of the split has a reduced resolution, capturing less ticks (which has implications for the PSE) and implying that a greater change in interval duration would be required to generate a tick count that could be discriminated (which has implications for judgement uncertainty).

Unlike a constant-rate stopwatch, a stopwatch with a decreasing rate also makes strong predictions about accuracy (measured here using the PSE) in split-interval conditions. If clock rate has declined following a break, on average less pulses will be accumulated in

the second half of a split interval compared with the same epoch within a contiguous interval. The result would be that the split interval should be perceived as shorter, which would manifest as an increase in the PSE. This prediction finds qualitative support in the results of the previous experiments (noted above). To investigate the possibility that timing can be paused with a slowing pacemaker we designed an experiment providing additional predictions specific to a slowing pacemaker. In addition to comparing whole and split target stimuli, the duration of the break between the two components of a split-target stimulus was manipulated (single interval; split interval-short pause [500 ms]; split interval-long pause [1,500ms]). A longer break should exaggerate the changes in precision and accuracy predicted by a slowing stopwatch, because tick rate will have declined even further across a longer gap. The focus is on precision rather than accuracy, in part because accuracy, typically measured as the PSE, is prone to shift dramatically for many reasons in interval timing tasks (e.g., Droit-Volet & Meck, 2007; Heron, Aaen-Stockdale, Hotchkiss, Roach, McGraw, & Whitaker, 2012; Johnston, Arnold, & Nishida, 2006; Penton-Voak, Edwards, Percival, & Wearden, 1996; Tse, Intriligator, Rivest, & Cavanagh, 2004; Wearden, Edwards, Fakhri, & Percival, 1998; Yarrow, Haggard, Heal, Brown, & Rothwell, 2001; Yarrow, Haggard, & Rothwell, 2004; Yarrow, Johnson, Haggard, & Rothwell, 2004; Yarrow & Rothwell, 2003; Zakay & Block, 1996). Indeed, it is almost harder to find an experimental manipulation that does not affect the interval timing PSE than one that does. Of particular concern here, the order of two judged intervals is well known to affect relative judgements about duration (the so-called time order error; see Hellstroem, 1985, for review) and additional substantial position-dependent biases emerge for short trains of >2 stimuli (e.g., Nakajima, Hoopen, & Van der Wilk, 1991; Rose & Summers, 1995). Therefore in the present experiment the standard interval was always presented first. This adaptation also tends to generate a higher degree of precision on interval timing tasks (Dyjas, Bausenhart, & Ulrich, 2012). So as to confirm that the effects within the initial two experiments were not specific to a

particular type of stimulus, the filled interval used in these initial experiments was substituted with an empty interval. This manipulation should also tend to increase interval timing precision (Grondin, 1993).

METHOD

2.2.1. Participants

A total of 24 participants took part in the experiment, 10 male and 14 female with a mean age of 31. Five of the initial participants were replaced (one due to a negative slope of the fitted function and four who generated outlying estimates i.e. >2 SD from mean).

2.2.2. Apparatus and Stimuli

The experiment was controlled by a PC sending digitized signals at 44,100 Hz using a 12 bit A/D card (National Instruments DAQ Card 6715). The correct timing of output signals was confirmed using a 20 MHz storage oscilloscope (Gould DSO 1604). Stimuli were 10 ms tones of varying frequencies (500 Hz/1,000 Hz/2,000 Hz) used to clearly demarcate the beginning and end of each empty interval (different frequencies were used to avoid confusion between the intervals to be timed and the gaps between them) presented via a small speaker placed in front of the participant. In split-target trials, the standard interval was marked by 1,000 Hz tones, the first component of the target interval by 500 Hz tones, and the second component of the target interval by 2,000 Hz tones. In single-target trials, the 2,000 Hz tones were omitted.

2.2.3. Design and Procedure

A 2 x 2 x 3 design included the between-subjects factor *timecourse* and two within-subject factors, *standard duration* (300 and 600 ms) and *target stimulus* (single interval;

split interval-short pause [500 ms]; split interval-long pause [1,500ms]). The standard duration stimulus was presented first followed by the target interval(s). The two separate *timecourse* groups received slightly different *interstimulus* intervals (see Figure 2.2). Group A received the standard followed by a 1,000-ms gap before the test(s), which meant there were differences in overall trial duration between the baseline, split-short, and split-long conditions. Because a potential source of variability in interval judgements can be attributed to memory, with noise potentially accumulating across the period for which an interval estimate must be maintained (e.g., Gamache & Grondin, 2010), in Group B the overall trial duration was held constant, achieved by inserting a long (2,000-ms) pause between the standard and the first target component when the gap between the two target components was short (500 ms), and a shorter (1,000 ms) pause when the gap was long (1,500 ms; see Figure 2.2). In both groups, the order of the three blocks (single interval, split interval-short pause, split interval-long pause) was counterbalanced across participants. The split-interval durations were randomly subdivided (the first part could be anywhere from 30% to 70% of the total with the second part making up the remainder). No feedback about correctness was provided.

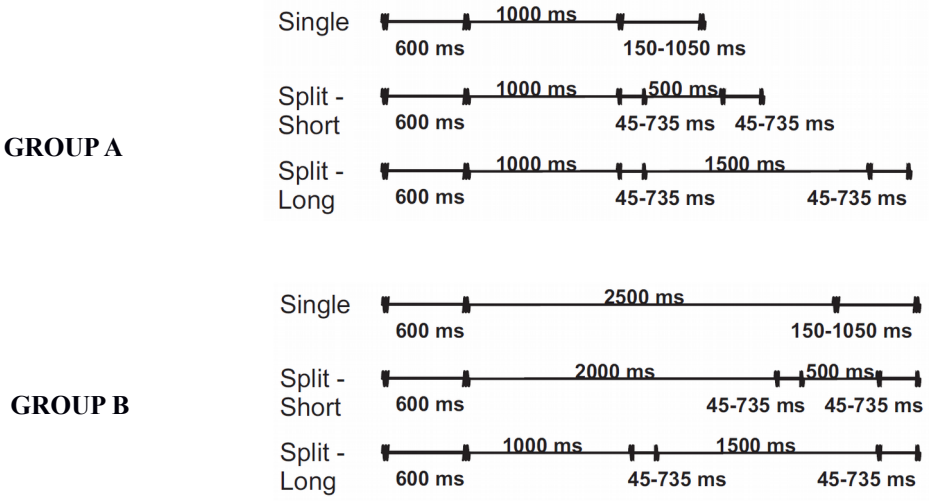

Figure 2.2 (Top) Illustration of the 600 ms standard conditions from Group A. The standard was presented first, in an empty interval task, and there were two variants of the double condition (split-short and split-long), which varied the duration of the gap between segments. (Bottom) Illustration of the 600-ms standard conditions from Group B. The time from the standard to the onset of the target was covaried with gap duration to equate overall trial duration.

2.2.4. Data Analysis

A maximum-likelihood cumulative Gaussian fit was obtained to the proportion of times that the target was judged longer than the standard for each tested target duration, using the Psignifit toolbox (Wichmann & Hill, 2001) in Matlab (MathWorks, Natick, MA). To measure variable error (i.e., precision), the standard deviation of the cumulative Gaussian ($\sigma^2_{observed}$) was estimated using the difference between durations required to yield "long" judgements 84% and 50% of the time. This value was the converted to judgement variance ($\sigma^2_{observed}$) by squaring. $\sigma^2_{Increase}$ was calculated by taking the average of four changes in $\sigma^2_{observed}$: from single to both split-short and split-long conditions, at standard durations of both 300 and 600 ms) and comparing with *c.* The scalar property states that scalar variance increases linearly with the square of the standard duration. Nonscalar variance was found by determining where a power function fitting the two relevant $\sigma^2_{observed}$ points (the 300 and 600 ms single target stimulus conditions) crossed the line x = 0 (i.e., the y-axis; see Figure 2.3).

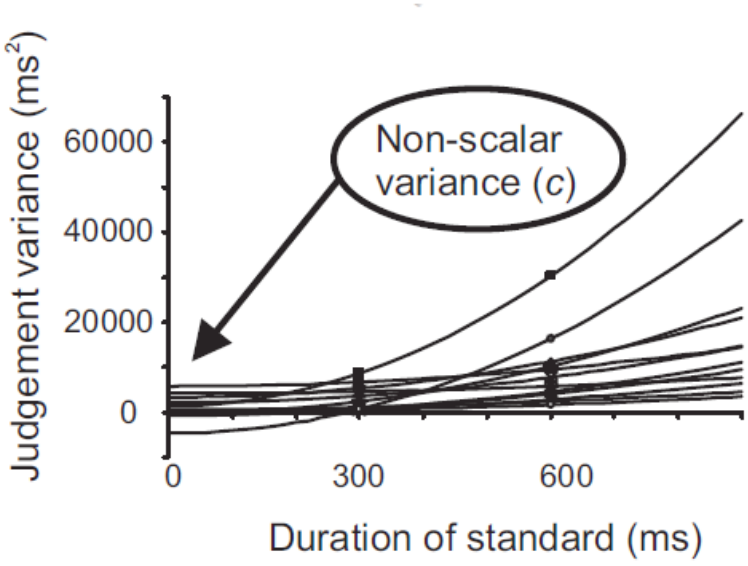

Figure 2.3. Judgement variance plotted separately for all participants in the single-target (baseline) conditions. Power functions are drawn through these data to reveal estimates of nonscalar variance.

The first analysis replicated the pilot studies, testing the predictions of a SET-like model, that the increase in variance should not exceed the non-scalar variance when a split-interval is introduced. The slowing-clock model was then simulated with Matlab. Taatgen et al (2007) provided the following formula describing how the inter-tick interval (t) of the clock evolves over time (p. 581):

$$\mathbf{t_n + 1 = at_n + noise\ (M = 0, SD = b \cdot\ at_n} \quad (2.5)$$

Here, "noise" indicates a logistic distribution with (M)ean of 0, and the model has three free parameters: *startpulse* (t_0, the initial value for the inter-tick interval), a (which controls the rate of slowing of the clock), and b (which scales the logistic noise). Because the slowing pacemaker model was originally validated against data from a task looking at much longer intervals (from ~2–21 seconds, where nonscalar variance makes a negligible contribution), it does not include a term to capture nonscalar variance. Hence for consistency with the overall framework, the model was slightly adjusted by adding a fourth parameter representing Gaussian noise in the (differential) delay to close/open the accumulation switch.

We maximum-likelihood fitted the slowing-pacemaker model to the σ2observed data from the two single-target conditions (i.e., from a typical interval comparison task, with 300 and 600 ms standards). This fit was obtained individually for each participant, with model predictions generated by simulating an experiment with 21 target levels × 10,000 trials per level × 2 standard durations. These simulations yielded trial-by-trial judgements which were then fitted with a sigmoid to extract σ2observed. Simulations at many different parameter combinations were tested to select best-fitting parameters using the Nelder & Mead simplex algorithm (Nelder & Mead, 1965; O'Neill, 1971). The best-fitting parameters were then used to predict σ2observed (and PSE values) for the split-short and

split-long conditions (separately for each participant, based on Monte Carlo simulations), assuming that the pacemaker continued to slow during the break. From these values the $\sigma 2_{Increase}$ was calculated (and ΔPSE) representing the predicted *change in variance* (and change in PSE) from single to split-short and split-long conditions (variance rather than SD changes were used in line with previously discussed experiments). Because the slowing-pacemaker model makes different predictions for split-short and split-long conditions, factorial ANOVAs were employed to compare model predictions with the data separately for different split durations and standard intervals.

RESULTS

The ability of a typical (constant rate) stopwatch to account for the loss of precision in split-interval conditions was tested first. The mean value of $\sigma 2_{Increase}$ significantly exceeded the mean value of *c* (46,522 vs. 3,535), $F_{(1,22)} = 10.42$, $p = .004$ (no effect of Group A vs. B or interaction with this factor). Hence the performance deterioration between the whole and the two split-interval conditions cannot be attributed to just the variance associated with switch operations.

Turning to a slowing-rate stopwatch – As the pulses become more distributed, the point of subjective equality should also change, and should increase, with a greater change emerging for a longer split (Figure 2.4). Points of subjective equality varied between short (300 ms) and long (600 ms) standard intervals, $F_{(1,22)} = 61.90$, $p = .001$. A slowing pacemaker successfully predicts that performance should decline, in terms of precision, from the short-split to the long-split condition. However, as the pulses become more distributed, the point of subjective equality should increase, opposite to what was

observed, i.e. instead of the split intervals being perceived as shorter they were perceived as longer.

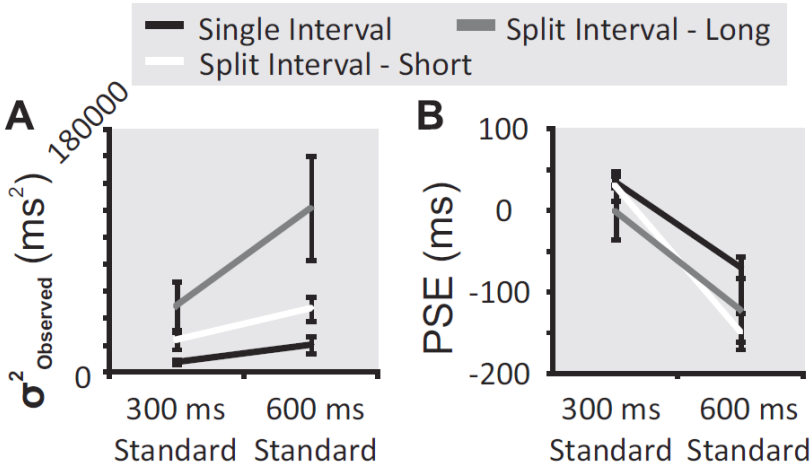

Figure 2.4 Mean judgement variance, and (b) points of subjective equality (shown as bias relative to objective equality = 0) averaged across participants. Error bars show standard error of the mean.

In Figure 2.4, data have been collapsed across Groups A and B as this between subjects factor was not significant and did not interact with any other factor in the ANOVAs. Judgement uncertainty (σ2observed) increased between the short (300 ms) and long (600ms) standard intervals, $F_{(1,22)} = 8.63$, $p = .008$, and more importantly, increased from whole to short-split (500-ms gap) to long-split (1,500 ms) conditions, $F_{(1.1,24.9)} = 8.40$, $p = .006$; linear trend $p = .005$. Hence the prediction of the slowing stopwatch model was confirmed, at least qualitatively, when considering precision. No other main effects or interactions were significant. To provide additional quantitative rigour, the slowing pacemaker model was tested by finding the best-fitting parameters for each participant in the single-target conditions, and then using these parameters to generate precise predictions for the split-interval conditions (which could be compared with the actual data). As expected, the model was able to provide a good fit to the single-target conditions (mean ± SD for predicted σ2observed of 77 ± 40 & 117 ± 67 ms for 300 ms and

600 ms standards, respectively, compared with empirical values of 79 ± 40 & 120 ± 79 ms). Considering the best fitting parameters themselves, mean estimates were a close match to those estimated by Taatgen et al. (2007) using a fit to a very different data set (11.4 ms, 1.19 and 0.014 for *startpulse*, *a* and *b* respectively in our data, compared with 11 ms, 1.1 and 0.015 in their fit, although this close match may have partly reflected our choice to use their estimates to initialize our parameter searches)[2]. An additional fourth parameter, reflecting nonscalar variance was likewise included - mean of 1,925 ms^2 (for the slowing stopwatch parameter fit) versus 3,535 ms^2 (for *c*).

Having obtained fits in single-target (baseline) conditions, model predictions were generated in order to assess how much precision should deteriorate (σ2Increase) and the PSE should shift (ΔPSE) when a short or long break in the target interval was introduced (i.e., in the short-split and long-split conditions). These data are presented in Figure 2.5, again shown for all 24 participants because the between-subjects factor (timecourse) was not significant and did not interact with any other factors. For precision (see 2.5A), the general trend is for mean decrements in performance that exceed the predictions of the model. An ANOVA comparing the empirical change in precision with the predictions of the slowing-stopwatch model revealed a significant main effect of model versus data, $F_{(1, 22)} = 5.03$, $p = .032$. Hence it can be concluded that a stopwatch that can be paused but has a slowing pacemaker does not predict the magnitude of decreased precision that was observed for sub-second intervals. There was also an interaction between this effect and the duration of the break, $F_{(1, 22)} = 4.40$, $p = .048$. The interaction indicates greater violations of model predictions in the long-split ($p = .033$) than the short-split ($p = .191$) conditions. For accuracy (ΔPSE; Figure 2.5.B), the divergence from model predictions is even more striking, with effects in the opposite direction to the model predictions. Here,

2 Although a longer value of *startpulse* was subsequently used by van Rijn and Taatgen (2008), this would not have been appropriate for experiments with much shorter intervals. A large value of *startpulse* generates steps in the psychometric function for short intervals, which are not generally observed, so a model parametrised this way is clearly designed to deal exclusively with longer intervals.

ANOVA revealed a significant effect of model versus data, $F_{(1,11)} = 148.13$, $p = .001$, with interactions suggesting that this divergence was more pronounced for longer breaks,

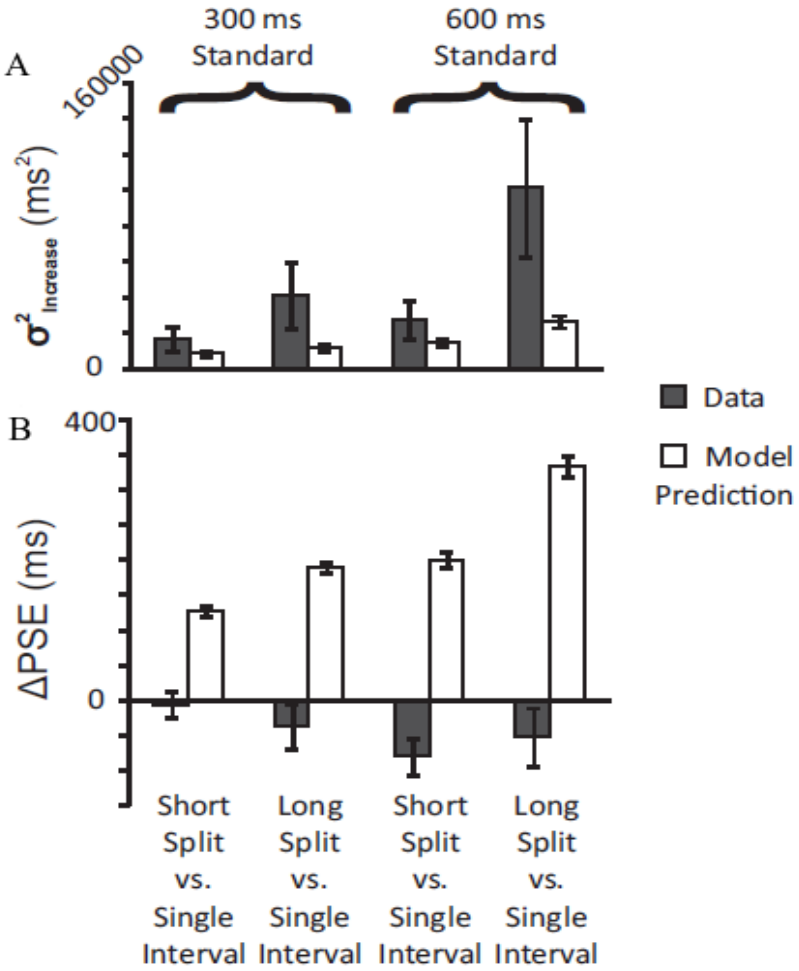

Figure 2.5 (A) Comparisons of the increases in judgement variance, and (B) changes in PSE with those predicted by an internal stopwatch with a slowing pacemaker (where tick rate continues to decline through the pause). Error bars show standard error of the mean.

$F_{(1,11)} = 19.52$, $p = .001$, and with longer standards, $F_{(1,11)} = 29.49$, $p = .01$. Hence, when considering both precision and accuracy, the data are not supportive of the notion of an internal stopwatch with a slowing pacemaker for intervals at sub-second timescales.

DISCUSSION

The results from the present study, akin to data obtained from the previously discussed pilot experiments, are a poor match to the predictions of a pacemaker accumulator

internal stopwatch that can be paused at will. Although lengthening the gaps in the split-interval task caused participants' performance to decline, as would be expected under a model with a slowing pacemaker, the target interval was perceived as longer than an unbroken standard, rather than shorter, which is in direct contrast with the results predicted by this model. This is likely, in part, to be a contextual bias resulting from the order in which standard and test were presented (i.e. a form of time order error). Hence, a fairer test might have been to attempt to remove the contextual bias on PSE before making any comparison with model predictions, perhaps by running conditions with standards in both initial and terminal positions and taking the average PSE shifts. However, even if we take into account the close association that exists between subjective duration and the context in which an interval is presented (e.g., Rose & Summers, 1995) and thus ignore the data regarding accuracy, the magnitude of the increase in judgement uncertainty (particularly prominent in the long-split condition) deviated significantly from model predictions suggesting a slowing pacemaker account is not sufficient to explain the observed results.

It has previously been shown that the ACT-R module with slowing pacemaker is able to predict behaviour in a variety of supra-second timing tasks (van Rijn & Taatgen, 2008) ranging from simple discrimination to the timing of multiple intervals, via a single timing mechanism. The results of this experiment question the ACT-R model applicability specifically for sub-second intervals. However, models are generally supplanted only when other accounts exist that can provide a better account of existing data. There is of course no shortage of potential models predicting a collapse of performance in split-interval conditions. For example, many models of interval timing do not employ a linear metric, and of particular relevance, many models do not offer any obvious system by which a timing operation could be paused. To take one prominent example, the striatal beat-frequency model (Matell & Meck, 2004) proposes that a population of neurons in

the prefrontal cortex act as oscillators, sending periodic signals to the striatum. Dopaminergic reward signals can generate a memory for a specific interval, equivalent to the coincident pattern of inputs that uniquely specifies that duration, via a mechanism of long-term potentiation. It seems implausible that the oscillatory activity of prefrontal neurons can be paused and then resumed from the saved state at will. Furthermore, there is no continuous metric for time in this model and thus no obvious way to perform temporal arithmetic: The coincident patterns that would specify each of two short intervals would have no consistent translation into the coincident pattern that would specify their sum. Hence the model predicts that performance should plummet in broken-interval conditions. A similar analysis could be applied to models based on exponentially decaying memory traces (Staddon & Higa,1999) or neural network dynamics (Buonomano & Merzenich, 1995).

At first glance, however, the data appear just as problematic for these models as they do for the SET or ACT-R models, because while performance certainly got a lot worse in split-interval conditions, most participants could still perform well above chance. Yet with a little thought, it is quite straightforward to come up with some plausible strategies by which an observer might achieve this level of performance without having to pause an internal clock. Some aspects relating to the observed results seem highly suggestive of strategic solutions. For example, while some degree of between-subjects variability in the ability to time intervals is to be expected, it is noticeable that this variability is greatly magnified in split-interval conditions compared with the single-target baseline condition. Clearly some participants were very much better able to handle split-interval tasks than others, to an extent that greatly outstripped differences in basic timing ability. This seems more consistent with differences in the ability to find a workable strategy than with all participants making the best use they can of the same hard-wired clock. Participants could have ignored the standard to treat the task as effectively a method of single stimulus

presentation. However, instead of attempting to compare just one component of the split interval to its own average across trials, participants might time the entire interval from onset of the first part of the split target to offset of its final component. The break duration was not randomised in the experiment and the total time would thereby give unambiguous information about this trial's target duration relative to previous trials' target durations, and splitting the target unequally does nothing to defeat an approach like this. This strategy forces the observer to time much longer intervals, which are subject to decrements in precision as per Weber's law. It predicts worse performance with a longer break in split-interval conditions, consistent with the obtained results.

Conceivably many other strategies could just as easily have been employed (e.g., timing just one target substimulus in the broken-interval condition and then attempting to run the clock two or three times in rapid succession during the subsequent standard interval, or performing a comparison between the longer of the split target's components and the standard, and responding "longer" if either substimulus on its own even approaches parity with the standard). It is thus evident that the space of possible strategic solutions to the split-interval task is very large, particularly when you consider that a given set of participants are probably mixing and matching different approaches, and that modeling any strategy implies specifying it in considerable detail such that parameterisation (or at least some judicious decisions during implementation) would tend to give even greater scope for success.

The seeming ability to take account of breaks has also been suggested by nonhuman animal work. Early studies (e.g., Roberts & Church, 1978) utilized a peak-interval (PI) procedure wherein animals receive reinforcement at the to-be-timed duration. Such studies have generally analysed the average response rate on peak (non reinforced) trials, so that responses beyond the point of reinforcement can be assessed. When the stimulus is

broken, it sometimes appears as though the animal subjects retain the pre-gap interval in memory and then resume timing where they left off, consistent with how one might expect a stopwatch model to function. However, such accurate performance is far from a certainty, and rats and pigeons also often behave as though their clocks continue to run straight through the gap, or indeed start again from scratch after it ends. For example, when the PI procedure was reversed (Buhusi & Meck, 2000) and the animals were required to time the absence of a signal, with the gap denoted with a stimulus, the results suggested that the entire timing process was restarted following the gap.

The results from the present study may seem at odds with previous work where humans have successfully interpreted broken intervals (e.g., Fortin & Tremblay, 2006; Fortin et al., 2009; Tremblay & Fortin, 2003). However, the crucial distinction between the aforementioned studies is their use of supra-second intervals. These would permit counting or subdividing strategies (Grondin et al., 1999; Grondin et al., 2004), a key reason why shorter durations were used in this study. Clearly, if one can count, one can ignore a gap even with a clock that cannot be paused. In conclusion, the results of this experiment revealed a decline in performance that greatly exceeded the calculated estimate for two kinds of pacemaker-accumulator model, suggesting that participants cannot pause and restart the accumulation of temporal pulses like a stopwatch when timing short intervals.

This chapter has provided an empirical challenge to models such as SET. The scalar property forms the foundations of models of this kind, and so the following chapter will explore whether any deviations from this property can be observed at different durations following an intensive training regime.

CHAPTER 3 – WEBER'S LAW

INTRODUCTION

Weber's Law, described as a ubiquitous phenomenon in sensory perception, was defined by Ernst Weber in 1830, who noted that the magnitude of judgement error scales linearly with the stimulus magnitude. This can be expressed as:

$$\frac{\Delta I}{I} = k \tag{3.1}$$

ΔI denotes the difference threshold, I is the stimulus intensity (or in the case of time perception, the interval duration) whilst k represents a constant of proportionality which remains consistent irrespective of any variations in I. Although best documented in sensory research, Weber's Law has also been observed to apply to a number of other behaviours including motion perception (Zanker, 1995), value perception (Namboodiri, Mihalas & Shuler, 2014) and decision making (Romo, de Lafuente & Hernández, 2004; Deco, Scarano & Soto-Faraco, 2007). Its application in time perception has been widely documented and it has served as a foundation for models of interval timing such as SET.

The scalar property, a form of Weber's Law, has frequently been observed in timing behaviours in both animals and humans. It encompasses two important features: Mean accuracy and the scalar property of variance. In the first instance, the estimated duration (i.e. the internal representation of the duration) has to proportionally correspond to the real duration. Secondly, as briefly discussed in the introductory chapter, timing sensitivity has to remain constant across varying durations. In other words, consistent with Weber's Law, such that the coefficient of variation (CV) (standard deviation / mean) remains

constant across timed durations. The CV is noted to be proportional to the Weber Ratio (also known as the Weber Fraction). Weber's Law is said to hold if the Weber Ratio remains constant over a set of durations or modalities. However, this is in fact a slight simplification in the case of time perception. Shorter durations usually have a higher Weber Ratio which decreases as the duration gets longer, to what has been termed as the plateau region (see Figure 3.1).

Many studies have supported the existence of approximately scalar timing in animals and humans (reviewed in Lejeune &Wearden, 2006; Wearden & Lejune, 2008). For example, Roberts (1981), who invented the peak procedure (whereby fixed interval trials, which reinforce a criterion duration at the time of response, and peak interval trials, where no reinforcement is given but the subject is nonetheless expected to respond at a specific time, are randomly interspersed – in the peak trials, the response distribution is then expected to converge around the studied duration with proportional variance) used it in an animal study to measure the response rates on a battery of time discrimination tasks. The data from the experiment were then further used in a comparative study investigating timing processes in humans and animals by Wearden and McShane (1988), who were among the first to demonstrate the applicability of scalar timing theory in humans. Data from the human participants, who were required to produce five durations (ranging from 500ms to 1300ms) was analysed in a similar manner as in the above noted peak procedure, and results revealed that both complied with scalar timing and Weber's Law. However, the application of Weber's Law to time perception has also been challenged, and a number of studies have found the Weber Ratio to increase as the interval gets longer in both human and animal studies (e.g. Crystal 2006; Bizo, Chu, Sanabria & Killeen, 2006; Getty, 1975; Lavoie & Grondin, 2004; Grodin, Laflamme, Bisson, Hasuo & Kuroda, 2011).

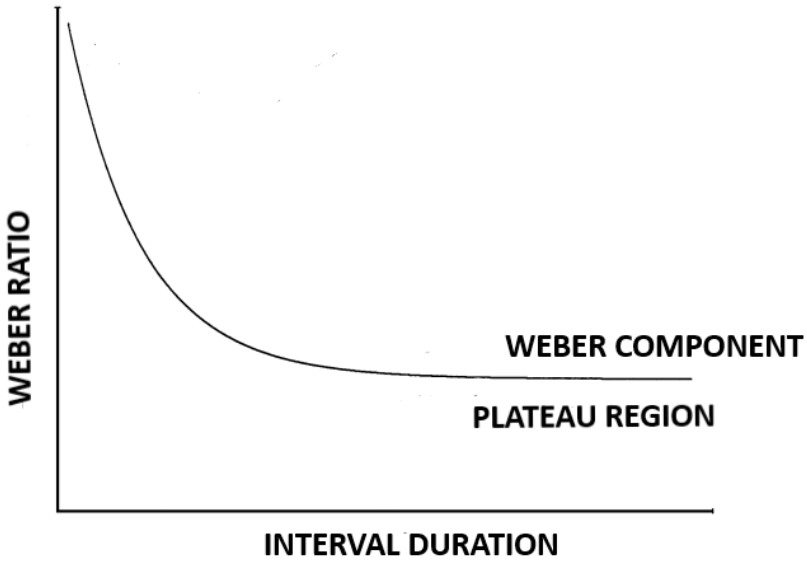

Figure 3.1. Weber Ratio, ΔI/I, vs. interval duration, I. ΔI/I is large for short durations. For longer durations of I, ΔI/I approaches a constant. This component has been called the "Weber component" because Weber believed that ΔI/I was universally constant. (modified from, Norwich, 2003).

The compliance of a dataset to Weber's Law may also to an extent be affected by the included range of data points i.e. the difference between the longest and shortest interval duration (Wearden & Ferrera, 1995; 1996; Ferrera, Lejeune & Wearden, 1997).

Nonetheless, as already alluded to, and illustrated in Figure 2.1, the generalised variant of Weber's Law allows for a source of noise unrelated to the interval duration which abates (in relative terms) as durations increase, thereby accounting for the sharp ascension in the Weber ratio observed with very short durations as noted by Getty (1975). He looked at duration discrimination in the range of 50ms to 3200ms (15 base durations) and proposed a constant monotonic increase in (non-normalised) threshold across durations, although in line with the generalised form of Weber's Law, he also noted that the Weber Ratio was higher for very short durations (equivalent to a non-normalised threshold of above zero for a notional base interval with zero duration).

The generalised version of Weber's Law for very short intervals is now fairly uncontroversial. However, Getty also observed deviations from Weber's Law in durations longer than 2000ms, specifically an increase of the CV. Reports differ in regards to the mentioned top boundary; some studies suggest that the cut-off is at 1500ms (Gibbon, Malapani, Dale & Gallistel, 1997) whilst results from animal studies indicate a maximum sensitivity of 1200ms (Crystal, 2006). Timing precision has often been observed within a particular range of interval durations in both animal (Crystal, 1999, 2001; Bizo, Chu, Sanabria, & Killeen, 2006) and human studies, with the highest noted sensitivity observed between 272ms and 800m (Fetterman & Killeen, 1990; Grondin, 1992; Drake & Botte, 1993; Collyer, Broadbent & Church, 1994; Friberg & Sundberg, 1995). Lewis and Miall (2009) utilised a very wide range of interval durations in a series of reproduction tasks, and although differences were noted between particular durations (e.g. higher precision in the 3000ms duration versus 600ms), no specific boundary points were observed. Bangert, Reuter-Lorenz & Seidler (2011) used a set of five durations ranging from 300ms to 1700ms to assess sensitivity and compliance with the scalar property. They also compared patterns of variability across the perceptual and motor domains. They found no significant correlations across the perceptual/motor tasks and also no convincing support for the notion of a single scalar clock working across different durations: Data from the experiments was observed to generally exhibit a U-shaped pattern (i.e. exhibited both the decrease and subsequent increase of the CV with increasing durations described above), with the CV well fit by a quadratic function.

Disparities in specific pairs of different durations in the Weber ratio have also been recorded, for example: Higher at 2000ms vs. 200ms (Lavoie & Grondin, 2004), and higher at 1000ms vs. 200ms (Grondin, 2010). These findings again disagree with the assumption that variability consistently increases linearly with duration (Gibbon, 1977; Gibbon & Church, 1984). Likewise as previously mentioned, very short durations (i.e.

below 250ms) have generally been found to not hold up to the traditional form of Weber's Law (Allan & Kristofferson, 1974; Fettermann & Killeen, 1992; Bangert, Reuter-Lorenz & Seidler, 2011).

In one of the most famous studies investigating the adherence of timing precision to Weber's Law, Kristofferson (1980) proposed a "time quantum" where temporal variability is explained in terms of temporal units or 'q', which remain constant for a range of durations, and any variation in interval perception follows a triangular distribution with base $2q$. Consequently, for intervals below 1500ms a quantal step relationship rather than a linear one was proposed (between base duration and the non-normalised discrimination threshold) whereby discriminating between two intervals relies on the difference between them rather than the absolute magnitude of the estimated durations (Allan & Kristofferson, 1974; Allan, Kristofferson & Wiens, 1971). The timing of an interval was noted to rely on counting these temporal units, and where an upper limit of the counter is reached, a doubling of q takes place. This occurs whenever the timed duration requires more counts than can be accommodated by the system. Kristofferson supported this idea by acting as the only participant in an unusually long experiment, assessing sensitivity early and late during practice (6000 trials per base duration) for each of 13 different base durations. Importantly, the deviations from scalar timing that Kristofferson observed (for intervals from 100 to 1480 ms) are not reducible to either (or both) of the two deviation patterns described so far: The generalised version of Weber's Law (i.e. decreasing CVs with increasing duration for short durations) or the tendency for the CV to increase above ~1 second.

Results from studies investigating this quantal hypothesis of timing have provided mixed results, as with a study conducted by Geissler, Schebera, and Kompass (1999) who employed simultaneity thresholds of apparent movement of stimuli, and concluded that

these reveal a quantum of approximately 4500ms. Ulrich (1987) examined a number of temporal order judgement (TOJ) predictions and found no support for the hypothesis. Most pertinently, Matthews and Grodin (2012) replicated Kristofferson's (1980) study, employing slightly different data collection and processing techniques, although they note that any disparities arising as a result of the method are negligible. They found little evidence for the step functions observed by Kristofferson in two new observers. They also questioned whether Kristofferson's data and conclusions truly reveal the step function in the first place; when thresholds based on pairs of comparison durations within his data (D2 vs. D3 & D5 vs. D6, each pair lying symmetrically around the base duration) are plotted separately, the pattern discussed by Kristofferson is not quite as clear and appears to depend only on the D2 vs. D3 but not the D5 vs. D6 stimulus durations. Likewise as discussed above, the distribution of the durations used within the experiment could affect sensitivity; Matthews and Grondin suggest that the results obtained by Kristofferson could be a reflection of his dataset rather than an accurate representation of the mechanisms involved in perceptual timing. Finally the authors note that the results obtained from their two participants (final Weber fractions of around 3 and 6%) fall on either side of Kristofferson's (around 5%), which suggests that the quantal step function is not merely a result of a certain level of performance. However, they do acknowledge that it is possible that with further training, the step function could emerge. The observed disparity could be at least partially due to Kristofferson's prior experience (1976, 1977) with these type of tasks, which would mean that he required a lesser amount of temporal training in order to achieve the "asymptotic performance necessary for the step function to emerge" (Matthews & Grodin, 2012). Their data likewise challenge the consistency of the Weber Ratio across durations, with one participant displaying a U-shaped curvature whereby the declining Weber ratio is consistent with the generalised version of Weber's Ratio, but the ascension noted in durations over a 1000ms is not. Likewise, deviations can

be observed with the second participant whose data show instability in the Weber ratio, particularly in the 740-910 ms range.

The exact relationship between base durations and precision in interval timing is critical, because adherence to this relationship is the first hurdle that any aspiring model of interval timing must pass. However, as illustrated by this short review, this relationship remains contentious. Although deviations from the generalised variant of Weber's Law are often reported, they are generally within the context of a single task, and the statistical significance of the deviations is rarely assessed. A key feature of a genuine deviation from scalar timing is that its pattern should emerge consistently across several tasks, at least within an individual. With this criterion in mind, two sets of tasks were used in the present experiment – standard interval discrimination and temporal deviant detection. With the former, a standard stimulus was presented to participants, alongside either a longer or shorter comparison interval, allowing for a gradient comparison on the emerging psychometric function to assess temporal sensitivity. With the latter, a single stimulus is presented on each trial, and the amount of yes/no (i.e. was this the long target, rather than the standard) responses are used to determine a d-prime measure based on classic signal detection theory. Data from both tasks were compared to assess whether performance at all durations is broadly compliant with Weber's Law, or shows correlated deviations from this prediction.

METHOD

3.2.1. Participants

Systematic deviations from Weber's Law may emerge only with extensive training (Kristofferson, 1980). Hence, due to the extensive training which was required for the

purpose of the experiment, the participant sample consisted of only 3 participants; two males (age; 24, 36) and one female (39).

3.2.2. Apparatus and Stimuli

The trials were conducted on a PC (with Samsung SyncMaster 1100MB CRT monitor) running on a Windows XP operating system. Experimental software was programmed in-house (C++) and used to present auditory stimuli. A standard USB computer mouse and keyboard were used to record judgements. Auditory stimuli were delivered via digitised signals at 44100Hz through a twelve-bit A/D card (DAQCard 6715; National Instruments). The correct timings of the auditory output signals were confirmed using a 20 MHz Gould DSO 1604 storage oscilloscope, and the auditory stimuli (10ms 1000Hz pure tones) were themselves presented via small speakers.

3.2.3. Procedure

3.2.3.1 Interval discrimination task

Fourteen sessions comprising of six to eight auditory interval discrimination task blocks were completed over a period of two months, totalling 96 blocks. Participants completed several additional tasks before and after this task, relevant to a separate research hypothesis, which are described in the following chapter. However, for the purpose of the current chapter, only the interval comparison data from the second half of this prolonged practice period was analysed, in conjunction with data from a deviant duration detection task, to ascertain compliance with Weber's Law (or the generalised version thereof) as well as whether the observed pattern of deviations is consistent across tasks.

Empty standard and comparison intervals (whereby the onset and offset of an interval is indicated by a beep) were presented one after another to participants who were required

to indicate which interval was the longer one. The standard duration was always presented first followed by the comparison. Eight standard durations were included in the training sessions; 71ms, 100ms, 141ms, 200ms, 400ms, 566ms, 800ms, 1131ms. Participants trained on one standard duration before moving on to the next. Each block included one of the eight standard durations repeated at 8 different comparison values: 0.86, 0.9, 0.94, 0.98, 1.02, 1.06, 1.1, and 1.14 x the standard, totalling 64 trials per block. Twelve blocks per standard duration amounted to 6144 trials across all standards (768 trials per standard; 96 repetitions at each comparison interval).

3.2.3.2..Deviant duration detection

A deviant duration detection was completed several weeks after the interval comparison task. The task is based on the classical signal detection theory (SDT) as originally described by Green and Swets (1966) which assigns responses to a combination of sensitivity and noise. Each trial consisted of a single stimulus duration, which could take one of only two possible durations; participants were required to respond as to whether it was the standard duration or a deviant (i.e. longer) duration (a multiple of the standard, based on the participant's own detection threshold; see data analysis section). The same standard durations as in the interval comparison task were used; 71ms, 100ms, 141ms, 200ms, 400ms, 566ms, 800ms, 1131ms, presented in separate blocks, with four blocks of 100 trials each for each standard duration, thus 3200 trials in total. Each standard duration was assessed before moving on to the next.

Feedback ('correct' or 'wrong') was provided on each trial for both the interval comparison and the deviant duration detection tasks.

3.2.4. Data Analysis

Data from each of the twelve blocks for the eight interval training durations (71ms, 100ms, 141ms, 200ms, 400ms, 566ms, 800ms, 1131ms) was subdivided into two six-block segments so as to differentiate between the first and second half of interval training. The data was then converted from absolute to relative values, i.e. the proportion of trials where the comparison was judged longer than the standard at each tested multiple of duration. A measure of the slope was obtained by applying a maximum-likelihood cumulative Gaussian Fit to the second six-block set of data for each standard condition. The Weber Fraction, defined as the difference from 84% 'longer' to 50% 'longer' responses, was recorded along with the point of subjective equality (PSE), which notes the point at which 50% of the comparisons are estimated to be longer. However, the analytic focus was on the Weber Fractions. In order to test for deviations from Weber's Law, each base duration was compared to the base duration just above it, i.e. 71ms to 100ms, 100ms to 141ms etc. An inferential test using bootstrap resampled data from the fitting procedure (by performing 4999 simulated resamples and fits of the observed data) was conducted to obtain a 95% confidence interval on the difference in Weber Fractions (yielding $p < 0.05$ when this interval did not include zero).

In the deviant duration task, the deviant duration in each block was based on each participant's average Weber Ratio estimated from the practice/comparison task, i.e. deviant = mean Weber ratio x standard. The numerical estimate of sensitivity was calculated using the sensitivity index d' (by looking at the number of hits – saying deviant when it was deviant – and false alarms – saying deviant when it was standard). As the deviant was always a constant proportion of the standard, d' should be constant across different standards if it complies with Weber's Law, or only increasing under the

generalised version. Further analytic methods, based on model fits, are described in the results section.

RESULTS

Data for the two tasks (interval discrimination and deviant detection) were analysed separately and then compared to ascertain whether any deviations from Weber's Law correlated across tasks.

As an initial test for deviations from Weber's Law, data obtained at each duration from the interval discrimination task were compared with the data for the standard duration above it (i.e. 71ms & 100ms, 100ms & 141ms, 141ms & 200ms, and so on) using inferential tests which utilised the bootstrap re-samples from the fitting procedure (as described in the data analysis section) to calculate a confidence interval on the difference in Weber ratios. Adjacent pairwise differences for all three participants are detailed in Table 3.1. Significant differences for all three participants were observed between a number of interval durations, which are not consistent with Weber's Law predictions. However, it must be emphasised that only Weber Ratio *increments* from lower to higher durations contradict the generalised version Weber's Law, which as previously noted, states that the Weber Ratio can only decline. These were observed between 141ms to 200ms for P2, between the 566ms and 800ms durations for both P1 and P2, and between 100ms and 141ms for P3.

Table 3.1 p values of pairwise differences for all the participants. Significant differences are in bold text, significant differences indicating deviations from the generalised version of Weber's Law are further annotated with an asterisk.

Interval Duration	P1	P2	P3
71ms to 100ms	.097	.284	.740
100ms to 141ms	**.039**	.231	**.014***
141ms to 200ms	.160	**.044***	**.001**
200ms to 400ms	.180	.311	.897
400ms to 566ms	**.001**	.427	.346
566ms to 800ms	**.043***	**.014***	.165
800ms to 1131ms	.070	.475	**.001**

The Weber Ratios were plotted for each standard duration and are presented individually for each participant (Figure 3.2, 3.3 & 3.4).

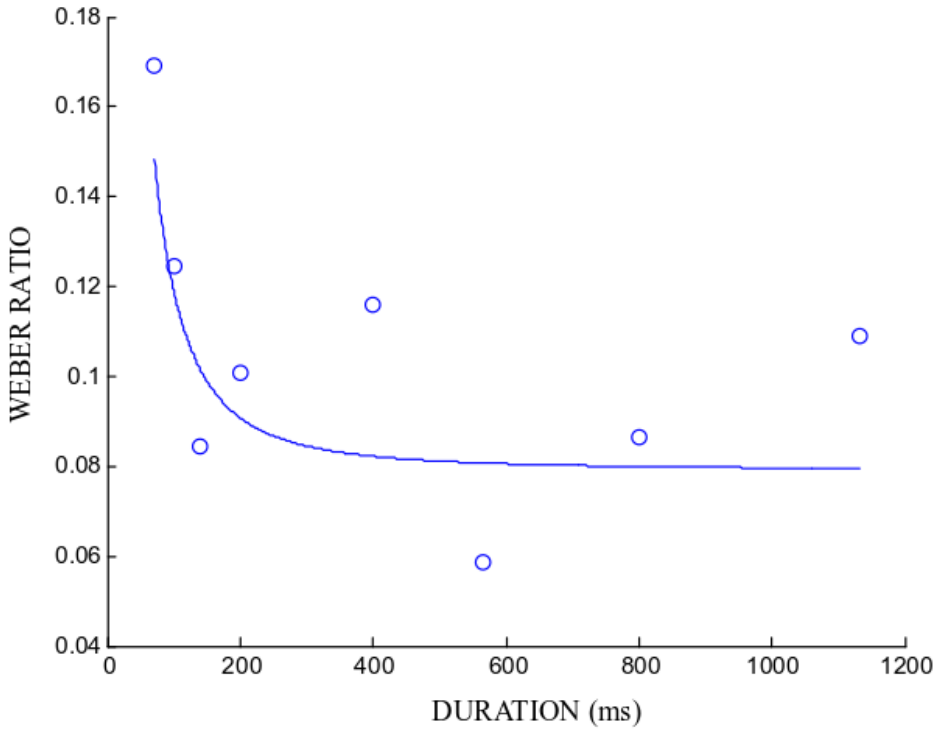

Figure 3.2 The Weber Ratio obtained from the second half of practice plotted against stimulus duration for participant 1.

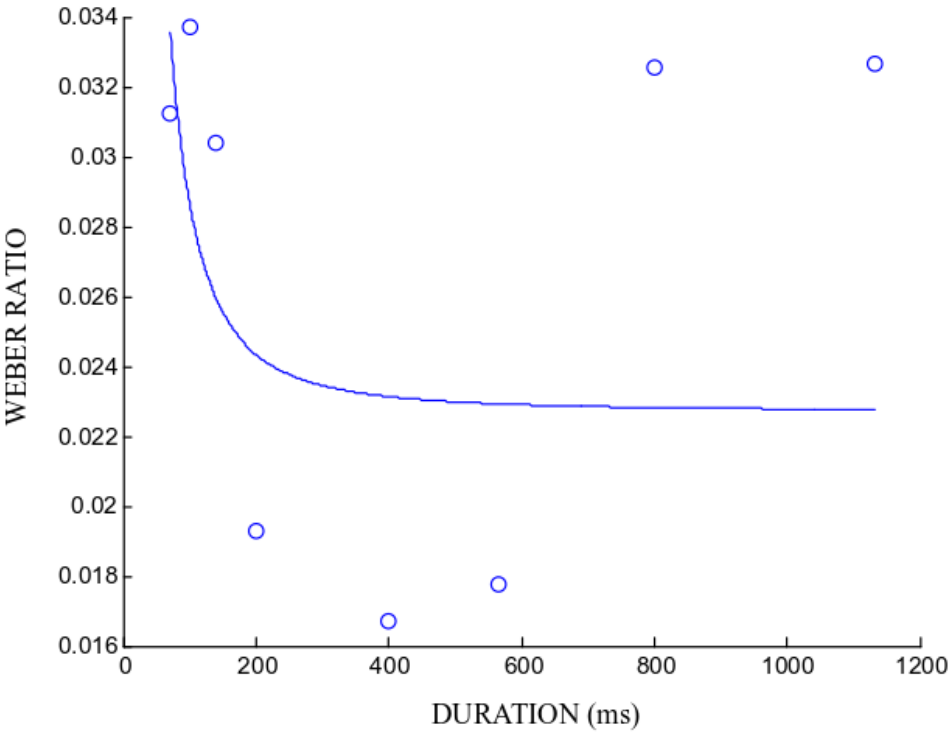

Figure 3.3 The Weber Ratio obtained from the second half of practice plotted against duration for participant 2.

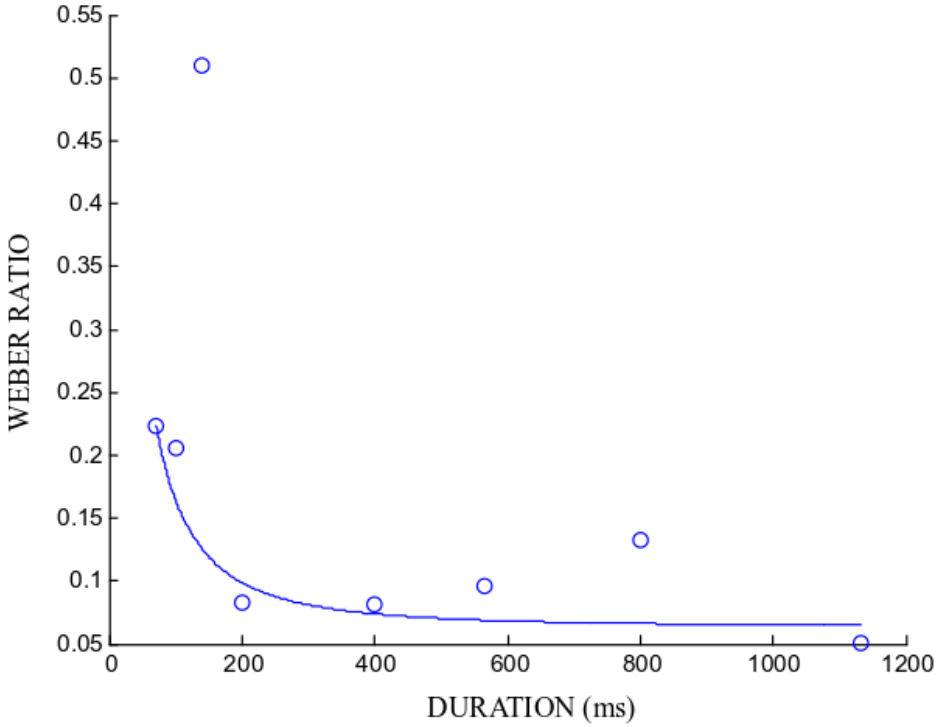

Figure 3.4 The Weber Ratio obtained from the second half of practice plotted against duration for participant 3.

A second set of analyses assessed commonalities in deviations from Weber's Law across tasks. The generalised version of Weber's Law predicts that the Weber Fraction should be a function of the base duration x:

$$\mathrm{WF}(x \mid s,n) = ((n^2 + (sx)^2)^{0 \cdot 5}) / x \qquad (3.2)$$

Within the equation *s* represents the scalar noise and *n* represents the non-scalar noise. This function was fitted to the data using maximum-likelihood methods, assuming normally distributed errors, but with a standard deviation estimated for each Weber Ratio from the bootstrap confidence interval.

The resultant best fit is shown by the solid line in Figures 3.2 to 3.4. Deviations from the model prediction (i.e. residual errors) across certain durations may simply be noise, or maybe systematic. To assess this, a similar model fitting procedure was applied to the second (deviant duration detection) task.

Data from the detection task were analysed using d' and plotted for each participant (Figures 3.5, 3.6 & 3.7). Under a generalised version of Weber's Law, d' is inversely related to the Weber Ratio, and thus should only go up as the duration increases. In a detection experiment where the target is always a constant proportion of the standard, d' should vary with the base duration *x* according to the function:

$$\mathrm{D'}(x \mid d,n) = xd / (x+n) \qquad (3.3)$$

Within the equation *d* is the maximum/plateau value of d' as the base duration tends to infinity, whilst *n* models the effect of non-scalar noise, and can be thought of as the base duration at which noise is coming equally from scalar and non-scalar sources. This

function was fitted to the data using maximum-likelihood methods, assuming Gaussian noise with a standard deviation estimated for each data point via standard formulas for the standard deviation of d'.

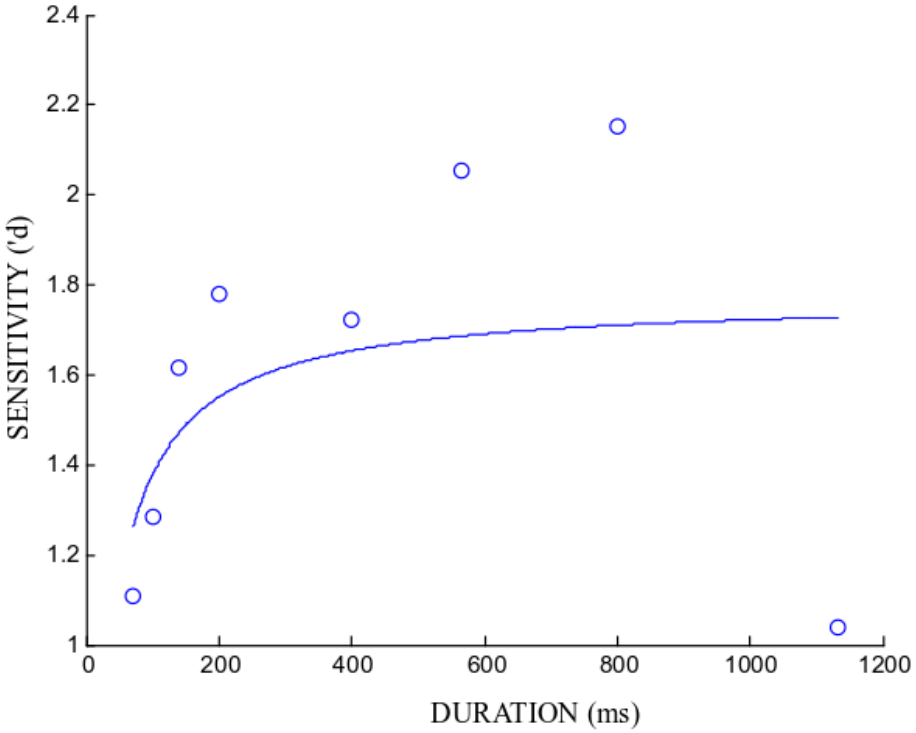

Figure 3.5. d' Prime plotted for participant 1.

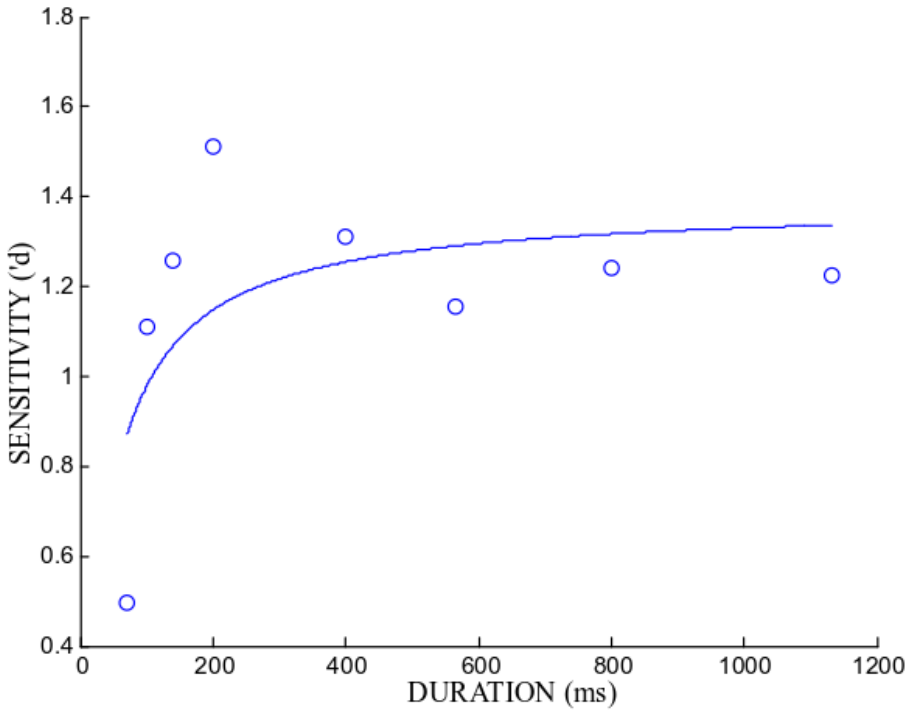

***Figure* 3.6.** d'Prime plotted for participant 2.

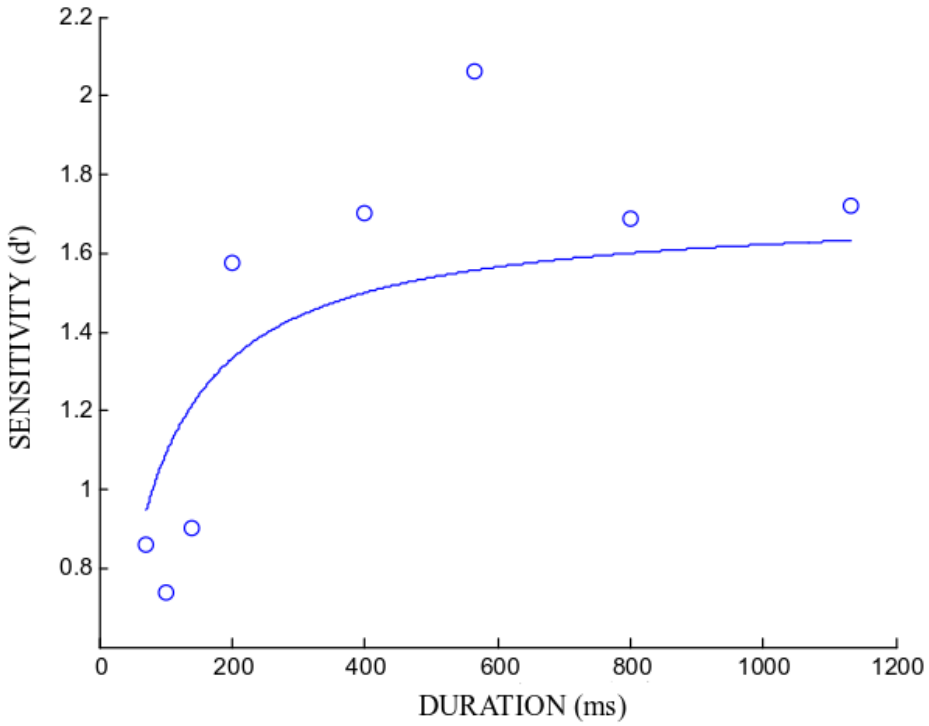

***Figure* 3.7.** d' Prime plotted for participant 3.

As can be seen in Table 1, which shows the degree of over/under performance relative to model predictions, certain parallels can be drawn between the different participants' performance as duration increased. Participant 1 performed worse than predicted by the best-fitting generalised version of Weber's Law model based on both the Weber Ratio and d' at the first two durations (71ms & 100ms), better than expected at the third duration (141ms) and sixth duration (566ms), and again worse than predicted at the longest duration (1131ms). A lesser degree of correspondence between tasks can be seen with participant 2 who performed better than expected in the fourth and fifth durations (200ms & 400ms) and worse at the two longest durations (800ms & 1131ms). Participant 3, similarly to participant 1, performed worse than expected at the first three durations (71ms, 100ms & 141ms), but better than expected at the fourth and last durations (200ms & 1131ms).

To check for consistency the d' residuals were compared to the Weber Ratio residuals; if there is a consistent pattern of deviation then a significant negative correlation should be observed between the differences. Although the correlations were found to be nonsignificant, they showed the predicted trend; for participant 1, r = -.587 (p = .126). A similar trend was observed for participant 3 (r = -.532, p = .174), whilst participant 2 had the least similarity between the tasks (r = -.0.98, p = .818). The chance of all three correlations going in the same direction like this is 1/8.

Table 3.2. d' and Weber Ratio Residuals

	Duration	**d'**	**Weber Ratio**
Participant 1	71ms	-0.1564	0.0209
	100ms	-0.0929	0.0054
	141ms	0.1419	-0.0167
	200ms	0.2304	0.0101
	400ms	0.0683	0.0338
	566ms	0.3662	-0.0219
	800ms	0.4398	0.0066
	1131ms	-0.6902	0.0295
Participant 2	71ms	-0.3761	-0.0023
	100ms	0.1309	0.005
	141ms	0.1891	0.0045
	200ms	0.3652	-0.0051
	400ms	0.0562	-0.0064
	566ms	-0.1343	-0.0052
	800ms	-0.0759	0.0097
	1131ms	-0.1134	0.0099
Participant 3	71ms	-0.0855	0.0002
	100ms	-0.3501	0.0407
	141ms	-0.3173	0.3851
	200ms	0.244	-0.0156
	400ms	0.2017	0.0072
	566ms	0.504	0.0277
	800ms	0.0898	0.0663
	1131ms	0.0894	-0.0143

DISCUSSION

The present analysis looked at the compliance of performance (specifically precision) at several durations with Weber's Law (including the generalised version). Furthermore, potential patterns of deviation from predictions across durations were investigated by comparing data from two separate tasks for each of the three participants.

Significant deviations from Weber's Law were observed for all three participants, although none displayed the quantal function as described by Kristofferson (1980). More importantly, noncompliance with the generalised version of Weber's Law (Getty, 1975) was also detected, with increasing Weber Ratios from shorter to longer durations at different stages for the three participants. Data from P2 and P3 revealed deviations between 100ms and 141ms as well as 141ms and 200ms, but these durations could be said to fall outside previously suggested boundaries of the noted, 400ms to 1450ms (Halpern & Darwin, 1982; Ehrlé & Samson, 2005) at which the Weber Ratio is noted to hold. However, the increasing Weber's Ratio between the 566ms and 800ms durations which was observed for both P2 and P3 is a clear violations of the scalar property. However, it should be noted that this finding was only visible for two of the three participants. Similarly, it must be acknowledged that the number of statistical tests which have been conducted increases the possibility of a type I error. Although the trend was not observed in the d' data, similar observations have been made by a number of other studies, so the present findings, although needing cautious interpretation, are consistent with previous literature (Drake & Botte, 1993; Lavoie & Grondin, 2004; Bizo et al, 2006; Grondin, 2010).

Deviations of this type pose a challenge for pacemaker-accumulator models such as SET, and the embedded timing module of the ACT-R, and could be an indication that

timekeeping might not be based on a *single clock* mechanism as posited by these models, but rather a result of a combination of factors or processes. Different explanations have been proposed by the different classes of models. Random process neuronal models based on synfire chains with different transmission times (Haß, Blaschke, Rammsayer & Herrmann, 2008) suggest that the pattern such as the one observed here is a result of a constrained optimisation process. Oscillator models such as the more generalised Striatal Beat Frequency model (Buhusi & Oprisan, 2013) propose that scalar errors are an emergent property of neuronal dynamics. Models of timing and their capacity to account for the current findings in the context of timing literature will further be discussed in the closing chapter (Chapter 6).

In line with previous studies (and violating the generalised version of Weber's Law), the Weber Ratio was expected to rise at the highest duration which is over 1000ms (1131ms). However, different trends were observed for each participant. The most practised participant (due to prior experience in experiments involving interval timing) was Participant 2, who was also the most precise overall. He showed a distinct U-shaped curve consistent with a number of previous experiments (e.g. Cantor & Wilson, 1981; Gibbon, 1997; Matthews & Grondin, 2012) ranging over a wide range of durations (milliseconds to hours). However, this pattern was not visible for the other two participants, and similarly this pattern was once again not mirrored for Participant 2 in the deviant detection task, which does not allow for a simple and consistent interpretation of the findings.

An increasing Weber Ratio at high durations has likewise been reported in a number of animal studies (Zeiler & Hoyet, 1989; Zeiler & Powell, 1994; Bizo, Chu, Sanabria & Killeen, 2006), although these utilised durations well over a 1000ms. Lavioe & Grondin (2004) used a set of intervals extending between 200ms and 2000ms in order to assess the

stability of the Weber Ratio across these durations. Temporal discrimination, whereby participants were required to estimate (without resorting to counting strategies) whether the presented interval was 'long' or 'short', was used. Results from the study revealed that in all four of the conducted trials the Weber Ratio was higher at 2000ms than at the 200ms duration. Lejeune and Wearden (1991) suggest that at very long durations, akin to very short durations, additional non-scalar processes come into play. A model (derived from Wearden, 1985) was fitted to their data, which scaled down the Gaussian growth process thereby controlling the so-called random responses (which were noted to exert a more substantial effect with longer, as opposed to shorted durations), and the authors were thereby able to maintain a constant CV across durations.

The compliance to Weber's Law across interval durations has previously been observed to vary depending on the range of data points used within a given experiment (Ferrera, Lejeune & Wearden, 1997; Wearden & Ferrara, 1995, 1996). Grondin, Bisson & Gagnon (2009) conducted an investigation looking at the extent of this effect. The range and distribution of comparison intervals and its impact on temporal sensitivity (and thereby the stability of the Weber Ratio) was assessed with two sets of comparison intervals. Two conditions were compared – a large versus a narrow spread of interval durations. Comparison intervals were separated by 2ms in the 'narrow' spread and 10ms in the 'large' spread (for the 200ms standard), and by 10ms and 50ms respectively (for the 1000ms standard). The CV for the 200ms condition in the 'narrow' spread was significantly higher than the CV for the 1000ms condition, although the same effect was not observed for the 'large' spread where the CV remained constant for both the 200ms and 1000ms conditions. A key finding of the study was that the *spread* effect hinges on the standard duration. The comparison durations within the current experiment ranged from 0.86 to 1.14 of the standard interval (8 in total), which allows for a reasonable spacing between the comparison intervals when compared to the above study, so this is

unlikely to be a consequential factor contributing to the observed rise in the Weber Ratio at higher durations.

Importantly, the two different tasks implemented in the current experiment were used to assess whether deviations from Weber's Law correlate at particular interval durations for each participant. It has previously been suggested that deviations from Weber's Law (or its generalised version) are not convincing when observed on a single task, as they may reflect idiosyncrasies of that particular task rather than timing in general (Wearden & Lejune, 2008). Consistent deviations on more than one task would therefore be much more convincing, and amenable to statistical confirmation, but have rarely been explicitly sought. Here, two of the three participants just missed reaching statistical significance on a test of this hypothesis, perhaps because of low statistical power, and although no significant relationship was noted, the modest association could be argued to point to some inconsistencies in Weber's Law. However, it must be noted that different durations were tested in a set order for both tasks, and so the possibility that the consistent effects are a result of transfer of learning being more pronounced from certain durations (to the successive one) must be considered. Although no specific duration was strictly observed to display maximal timing sensitivity, it is possible to speculate that a clearer pattern in regards to both findings could be obtained with a larger sample. Studies have provided varying reports in regards to optimal timing sensitivity, spanning from 300ms to 800ms (Drake & Botte, 1993; Friberg & Sundberg, 1995). However, Grondin, Oullet & Roussel (2001) who specifically looked at durations ranging from 500ms to 740ms found no such effect. As noted by the authors, if timing sensitivity is delimited to any particular range, factors such as individual differences and task demands are also likely to play a part.

Violations in Weber's Law encountered in previous studies and to a certain extent observed in the present experiment, could be an indication that temporal calibrations are

governed by factors additional to the well-known scalar timing law. The noise which is a significant component at every stage of the timing process accumulates but is said to level out with longer durations, although as noted in the current study, the results are not entirely supportive of this claim. Another problem arises when one considers the neural underpinnings which might regulate these processes, as inference from psychophysical findings to neural mechanisms is not clear cut. Haas (2012) used an information-theoretical approach to consider the underlying processes and compliance to Weber's Law in timing. A computational model of neural processes which render time-dependent operations in line with psychophysical predictions was utilised. Their findings indicate a compliance to Weber's Law only "if the estimate is based on temporal changes in the variance of the process." A more complete assessment can only be achieved if the circumstance of each Weber's Law deviation is documented in line with the precise nature of the observed errors in timing. Currently, we appear some way distant from a model that captures all of the (potentially idiosyncratic) deviations from Weber's Law that may exist.

The following chapters will focus on the underlying architecture of interval timing by looking at any potential commonalities between interval timing in different modalities and at different durations.

CHAPTER 4 – TRANSFER OF LEARNING

INTRODUCTION

Enhanced performance on a variety of basic perceptual tasks as a result of training has been widely documented (e.g. Ball & Sekuler, 1967; Fiorentini & Berardi, 1981; Gaffan, 1996; Ahissar & Hochstein, 1997). Often, these improvements are restricted to the trained task and the gains do not transfer to similar perceptual tasks (Karni & Bertini, 1997; Sagi,2011; Green, Kattner, Siegel, Kersten, & Schrater, 2015). The specificity of the resultant learning has revealed localisation constraints and further elaborated on the neural basis of the underlying processing. Transfer of learning in the temporal domain has likewise provided important insights into the underlying neural architecture supporting different timing behaviours. This methodology enables further investigation of the mechanisms which support interval timing. If generalisation across different features (e.g. duration, modality etc.) is noted, this would indicate a central or at least a partially shared timer. The current chapter discusses the findings of a number of transfer of learning studies in the temporal domain. Perceptual learning and generalisation is further investigated with a battery of tasks which include motor and perceptual tasks utilising a large set of durations.

Comparably to other perceptual learning, training on interval timing tasks has been observed to improve performance. Extensive practice on thirteen base durations (100ms, 160ms, 200ms, 250ms, 350ms, 450ms, 570ms, 740, 800ms, 910ms, 1080ms, 1180ms, 1480ms) was undertaken in a study by Kristofferson (1980). The training consisted of 260 sessions. Each session was made up of 300 trials and focused on a single base duration at a time in an ascending order. A rapid threshold decrease was observed in the first six sessions, although this was noted to plateau towards the end, particularly when the task

demands increased. Group analysis of all the trained durations revealed a practice effect, although details regarding gains at each of the base durations were not reported. Matthews and Grondin (2012) performed a direct replication study of Kristofferson's experiment and found improvement on the base durations in the first two days of testing, with a gradual and mostly linear progress towards the end of the testing phase. The authors conclude that a relatively modest improvement was obtained, mostly restricted to the longer durations. An earlier study by Rammsayer (1994) exploring potential differences in interval learning (using energy dependent cues – filled and empty intervals as well as stimulus intensity) found no practice effects in either condition.

The amount of training which was undertaken by the latter study is considerably less when compared to other studies investigating temporal learning and generalisation (see Table 4.1). The study by Kristofferson as well as later experiments such as the one by Matthews and Grondin, found that the threshold rapidly declines at the onset of training and then reaches a plateau after a set amount of trials. This indicates that the gains in performance are garnered relatively early in the training processes. Nonetheless, according to Wright and Sabin (2007), approximately 360 training trials per day are required to achieve successful learning in interval discrimination tasks.

Although there are numerous studies which point to task-specific learning in timing, there are others which reveal transfer to different tasks which still involve interval timing but include altered non-temporal components (see Table 4.1.for a summary of several transfer of learning studies which include temporal and non-temporal components). Tonal frequency and interval duration were investigated in one such study (Wright, Buonomano, Mahncke & Merzenich, 1997).

Intensive training on an auditory interval discrimination task, using a 100ms base duration with a tonal frequency of 1kHz, was completed by participants (900 trials per day over the period of 10 days). Data revealed a significant decrease in the discrimination threshold, likewise learning benefits were found to remain at the trained 100ms duration coupled with an untrained frequency of 4kHz. But no improvements in performance were observed in any of the untrained durations (50ms, 200ms, 500ms) when bounded by the 1kHz tonal frequency.

Table 4.1. Summary table of generalisation studies, detailing task, interval type, trained duration range, amount of training, the presence of learning and generalization. (AP) adaptive procedure, (CS) constant stimuli, (S) single stimulus presentation, (F) filled intervals, (E) empty intervals, (Y/N/P) yes/no/partial. [1] Transfer to durations in close proximity to the standard interval. [2] Audiovisual to visual generalisation only. [3] Transfer to retinotopic location & orientation but not frequency. [4] Auditory to visual but not visual to auditory transfer.

Study	Trained task	Interval type	Trained durations	Number of trials (days)	Learning	Generalisation details	Transfer to untrained durations	Transfer to modality/other temporal task at same duration	Transfer of non-temporal components
Rammsayer (1994)	Auditory interval discrimination (AP)	E/F	50ms	1000 (20)	N	Interval type & stimulus intensity	N	–	Y
Wright et al (1997)	Auditory interval discrimination (AP)	E	100ms	9000 (10)	Y	Tonal frequency	N	–	Y
Nagarajan et al. (1998)	Somatosensory interval discrimination (AP)	E	75ms-125ms	9000-14400 (10-16)	Y	Auditory interval discrimination	Y[1]	Y	Y
Meegan et al. (2000)	Auditory interval discrimination (AP)	E	300-500ms	2500 (9)	Y	Interval reproduction (motor)	N	Y	–
Karmarkar & Buonomano, (2003)	Auditory interval discrimination (AP-S)	E/F	100-200ms	7200 (10)	Y	Tonal frequency	N	Y	Y
Van Wassenhove & Nagarajan (2007)	Temporal modulation rate discrimination (CS)	E	200ms	2400 (3)	Y	Auditory interval discrimination / tonal frequency	–	P	N
Planetta & Servos (2008)	Somatosensory interval discrimination (AP)	E	500ms-800ms	5000-10000 (10-20)	Y	Interval reproduction (motor)	N	Y	–
Bartolo & Merchant (2009)	Auditory interval production (CS-S)	E	450ms-850ms	7200 (8)	Y	Visual and auditory interval production	Y	Y	–
Lapid et al. (2009)	Auditory interval discrimination (AP)	E/F	100ms	3000 (5)	Y	Visual interval discrimination / interval type	Y	N	Y
Wright et al (2010)	Auditory interval discrimination (AP)	E	50ms-100ms	1800,3600, 9000 (2,4,10)	Y	Auditory interval discrimination / tonal frequency / interval type	N/N/N	–	N/Y/Y
Alais & Cass (2010)	Auditory / visual / audiovisual temporal order judgement task (AP)	F	300ms-500ms	640(8)	Y	Visual /Audiovisual / auditory TOJ. Tonal frequency/ retinotopic location & orientation	–	Y[2]	Y[3]
Grondin & Ulrich (2011)	Auditory interval discrimination (CS-S)	E	250ms	2520 (1)	N	Visual interval discrimination	–	N	–
Bratzke et al. (2012)	Auditory /visual interval discrimination (CS-S)	E	100ms-200ms	2560 (4)	Y	Visual / auditory interval discrimination	N	Y[4]	–

Similarly to Wright et al, the specificity of temporal and non-temporal components was assessed by Karkamar & Buonomano (2003). Here, participants were presented with only a single interval in their training phase, and the required response was based on a comparison to the standard interval presented prior to the training block. After familiarising themselves with the standard, they then had to decide whether the presented interval was longer or shorter than the given standard. Participants were trained on a 100ms/1kHz empty interval, but transfer was assessed to a 100ms/1kHz filled interval, a 100 ms/3.75kHz empty interval, and a 200 ms/1 kHz empty interval. So as to ensure that any effects were not restricted to learning the 100ms duration, a different set of participants trained on a 200ms/1kHz interval (test conditions: 100 ms/1kHz, 200 ms/1kHz, 200 ms/3.75kHz). Data were consistent with the results of many other studies whereby the frequency and interval type (i.e. empty vs. full interval) were found to generalise, although no practice effects were passed on to untrained durations. Ahissar & Hochstein (1997) had previously demonstrated that the type of training task which is undertaken has a considerable impact in regards to the features which are generalised as a result of the learning. With this in mind, Karkamar & Buonomano included an additional component in the second part of their experiment – the impact of task difficulty on learning. Here participants trained simultaneously on two intervals (50-msec/1-kHz and 200-msec/4-kHz training conditions;50 msec/1 kHz, 50 msec/4 kHz, 200 msec/4kHz, and 200 msec/1 kHz test conditions). Significant practice effects for both intervals were noted for 55% of the participants, 30% improved on one duration only with the remaining 15% showing no improvement. Akin to the first experiment, transfer to an untrained frequency was observed. Despite the increased task difficulty, the results parallel the initial finding whereby non temporal components are not affected by temporal learning and generalise to the learnt duration.

Generalisation to different modalities has been the focus of a number of investigations. Somatosensory interval discrimination was observed to show a complete transfer of learning to interval durations trained in the auditory modality (Nagarajan, Blake, Wright, Byl, & Merzenich, 1998). A partial transfer to durations close to the standard duration was also noted (i.e. 125ms vs. 100ms but not 125ms vs. 50ms or 200ms). Studies investigating transfer of learning from audition to vision have had mixed results; the majority have shown limited or no generalisation. An assessment of generalisation from an auditory interval discrimination task to one comprised of the same durations, except that in the latter the intervals were demarcated with visual flashes rather than auditory beeps, was conducted by Lapid, Ulrich and Rammsayer (2009). In addition, transfer between empty and filled intervals (auditory) was also investigated. This study also included a control group which is not a consistent factor in transfer of learning studies, although the controls only took part in the cross-modal condition. Similarly to previous literature, generalisation was not affected by interval type but in contrast, a transfer to an untrained duration was observed (trained empty interval of 100ms to 500ms). As the control group did not take part in the auditory interval type condition, it is not possible to fully verify that the results are not simply due to learning occurring during the pre-test stage. No cross-modal transfer was observed, akin to the control group which might indicate that vision and audition rely on separate interval timing mechanisms.

A similar study (Grondin & Ulrich, 2011) which examined transfer from an auditory interval discrimination task to the visual modality. This required participants to complete at total of 2520 trials, which is more or less comparable to the amount of practice trials in the above discussed study (3000) although these were all completed on the same day with 5 minute breaks between each session. A control group who completed the visual pre and post-test was also used. The effect of individual differences added a significant amount of noise to the data and so a jackknife method (a resampling technique which revolves

around an aggregated psychometric function as opposed to individual functions) was applied to the data. Although some improvement in the post-test was observed this was the case for both the experimental as well as the control group. The training schedule, as acknowledged by the authors, could have potentially affected the results as all of the training was undertaken in a single day. In contrast, generalisation from an auditory interval discrimination to a visual interval discrimination task was observed in a later study (Bratzke, Seifried, & Ulrich, 2012), although the cross-modal effect was not observed in the other direction (i.e. visual to auditory). This asymmetric result could be, as noted by the authors, explained by the auditory advantage in timing when compared to timing in the visual modality (e.g. Goldstone S, Goldfarb, 1964; Wearden, Edwards, Fakhri & Percival, 1998; Penney, Gibbon & Meck 2000; Ortega, Guzman-Martinez, Grabowecky & Suzuki, 2014).

The vast majority of studies investigating transfer of learning in timing utilise perceptual timing such as standard interval discrimination during the training phase. Bartolo and Merchant (2009) on the other hand used a production paradigm whereby participants trained on a visual and auditory single interval production task using one of three standard values (450ms, 650ms & 850ms). Participants were assigned to one of six groups, two groups per each standard interval were used, as this allowed for some variation in the test intervals (6 test intervals per group spaced relatively closely around each standard interval). The learning period was found to proceed at a similar rate to previous studies investigating auditory and somatosensory interval discrimination (Kristofferson 1980; Wright et al. 1997; Nagarajan et al. 1998; Karmarkar & Buonomano 2003). Practice effects were observed in all conditions and were noted to generalise to some of the non-trained intervals. Generalisation across non-trained durations was lowest in the 650ms condition. As noted by the authors, previous studies (Collyer, Broadbent & Church, 1992; 1994) have shown a preference towards specific durations during tapping

tasks with a significant bias around 650ms which, similarly to the above discussed studies, points to duration-specific neural mechanisms. An inter-modal transfer was also noted although the visual stimuli were reproduced shorter than the same intervals defined by auditory markers. This is in line with studies which have consistently found that auditory intervals are deemed longer than visual stimuli of an equivalent duration (Goldstone and Lhamon 1974; Wearden, Edwards, Fakhri & Percival; 1998; Grondin 2001).

In addition to considering transfer effects for purely perceptual or purely motor timing, one can also consider transfer between these kinds of task. Several imaging studies have detected activation of the same cortical structures in perceptual timing to those which are engaged in the coordination of movements and other associated components of motor timing which would suggest that training benefits could similarly be shared (Schubotz, Friederici, & von Cramon, 1999; reviewed in Wiener, Turkeltaub & Coslett, 2010). Indeed, when two groups of participants completed training on an interval discrimination task using one of two standard durations (300ms & 500ms) the results revealed significant transfer effects to motor timing (an interval reproduction task) although the reduction in variability was once again bound to the learned duration (Meegan, Aslin & Jacobs, 2000).

Although temporal discrimination is the task most often employed in temporal learning and generalisation studies, other tasks and procedures have also been utilised. Temporal order judgement (TOJ) tasks, whereby participants are required to make a judgement on the order of presented stimuli, were used to assess learning generalization between vision and audition. Three groups of participants were trained on an auditory, visual or an audiovisual TOJ in an experiment conducted by Alais & Cass (2010). Unlike the above discussed experiment by Wright et al which used interval discrimination, training on the

auditory TOJ didn't provide any practice effect to a different frequency in audition, but in line with a number of other studies it likewise didn't carry over to vision (nor the cross-modal task). Similarly, no generalisation in the other direction (vision to audition) was observed. The audiovisual task however improved performance in the visual TOJ but not the auditory one, despite previous studies recording a higher level of accuracy in performance on auditory as opposed to visual TOJ's (e.g. Alais & Burr, 2006). The authors suggest that the disparity is due to a temporal difference in sensory signals whereby improvement of the transmission capacity is mainly on the less precise modality (i.e. vision), resulting in the bimodal transfer effect being more prominent in vision rather than audition. It is unclear whether that is sufficient to fully explain this observation but it is known from previous studies that when different perceptual stimuli are conjointly learned they can either aid or interfere with each other depending on task, modality and attention (Nagarajan et al, 1998; Seitz, Yamagishi, Werner, Goda, Kawato & Watanabe, 2005; Robinson & Sloutsky, 2013).

Most transfer of training studies looking at temporal tasks have focussed on behavioural measures. By contrast, brain plasticity as a response to temporal learning was investigated using magnetoencephalography (MEG) measurements pre- and post-training by Van Wassenhove and Nagarajan (2007). Training was composed of temporal discrimination – a modulation rate task (5Hz modulation tone train), which assessed the discriminability of the rate of modulation using four tone beeps with a 200 ms stimulus onset asynchrony (SOA).

Comparison stimuli likewise consisted of a four tone train modulated at variable rates of 5.03125, 5.0625, 5.125, 5.25 or 5.5 Hz, i.e., from SOA of 198ms to 181 ms). Transfer of learning to a frequency discrimination as well as an interval discrimination task was a further component included in the experiment. Improved performance on the modulation

rate task was observed in the post training phase. This finding was accompanied by a change in the cortical processing of the learned stimuli in the post-test, the plasticity noted to arise as a result of training. These findings are in line with previous studies assessing neural changes to trained stimuli (e.g. Cansino & Williamson, 1997; Menning, Roberts & Pantev, 2000). In addition a partial transfer to some temporal intervals in the interval discrimination was observed although no transfer to an untrained frequency was noted. The lack of transfer in the latter and the only partial transfer to the interval discrimination task could potentially be a result of insufficient training. The training schedule and the amount of trials completed during the training stage was sufficient to promote learning although as can be seen in Table 4.1, it is not comparable to the amount of training in studies which observed generalisation (e.g. Wright et al, 1997).

The current literature investigating transfer of learning for temporal tasks has thus revealed mixed results. Transfer to untrained durations is not usually observed, but there is some evidence of transfer to nearby durations. Based on these studies, it is assumed that duration specific mechanisms underlie interval timing although in the latter case this specificity could function over a set range at each interval stage which could further be susceptible to training, resulting in decreased sensitivity as a function of the trained interval (Bartolo and Merchant, 2009). Transfer from perceptual to motor timing has likewise been observed (Meegan et al, 2000; Planetta & Servos, 2008) and it is likely that overlapping mechanisms may underlie these timing behaviours. Neural regions such as the cerebellum for example have been found to play a role in both perceptual and motor timing which could explain the observed generalisation (Ivry & Keele, 1989).

In the current experiment, participants trained on an interval discrimination task at eight standard durations ranging from 71ms to 1131ms. Prior to training a baseline at all tasks and durations was established. An assessment of any practice effects was applied to a

wide set of both trained and untrained durations, from the very low (35ms) to the very high (2263ms). The range of trained and test intervals exceeds the amount generally used in temporal learning investigations. Although Kristofferson's (1980) study utilised a large set of intervals, transfer to durations below/above the trained set was not examined. Similarly, the inclusion of several other tasks including motor timing (tapping & reproduction) and TOJ provides an additional element which has not previously been explored to the extent attempted here. Generalisation of temporal learning to a modulation rate comparison task has, to my knowledge, only been documented in the above discussed study (Van Wassenhove & Nagarajan, 2007) with no experiment having investigated the transfer heading in the opposite direction (i.e. from an interval discrimination task to modulation rate discrimination). Furthermore, here a non-temporal control task (line-length) allows a disassociation between temporal and non-temporal components of interval discrimination, as it could potentially reveal any incidental / general-purpose learning (e.g. learning how to retain magnitudes in short-term memory) as distinct from learning specific to temporal processes (such as a less variable pacemaker). The control task has been matched to the experimental tasks insofar as the task demands are concerned. Additionally, the inclusion of control participants who completed some of the pre- and post-tests allowed for additional verification in that any observed performance enhancement was due to the undertaken training. Generalisation across different durations or transfer between tasks at the trained duration would be indicative of shared or overlapping timing mechanisms underlying interval timing. If the findings of the present experiment correspond to the majority of previous studies, it is expected that partial transfer to other modalities will be observed although no transfer to untrained durations is expected.

METHOD

4.2.1. Participants

Due to the extensive training which was required for the purpose of the experiment, the participant sample consisted of just 3 participants; two males (aged 24 & 36) and one female (39). Additionally, 2 control participants, both male (aged 24 & 27) who did not undertake any intervening training between the pre and post-tests took part in just the tapping and reproduction tasks.

4.2.2. Apparatus and Stimuli

The trials were conducted on a PC (with Samsung SyncMaster 1100MB CRT monitor) running a Windows XP operating system. Experimental software was programmed in-house in C++ and used to present auditory stimuli. A standard USB computer mouse and keyboard were used to record judgements. Auditory stimuli were delivered via digitised signals at 44100Hz through a twelve-bit A/D card (DAQCard 6715; National Instruments). The correct timings of the auditory output signals were confirmed using a 20 MHz Gould DSO 1604 storage oscilloscope and the auditory stimuli (10ms 1000Hz pure tones) were themselves presented via small speakers. Data from the reproduction and tapping tasks were recorded with a precision to one millisecond, using a twelve-bit DAQPad 6015 A/D card (National Instruments) connecting the computer to a digital switch, in the form of a hand pedal. An adjustable chin rest was used to ensure equal distance from both speakers in pre and post-practice tests.

4.2.3. Design and procedure

4.2.3.1. Pre- and Post-Test Conditions

Pre- tests for all tasks – TOJ, line-length, tapping, interval reproduction and rate comparison as well as the interval comparison task at all 13 test intervals – were completed by the three main participants. Participants (excluding the controls) trained on a subset of the test intervals. After the training stage, post-tests were run on the same tasks to assess any training benefits (for the trained intervals) and transfer of training (for additional timing tasks and untrained intervals). The standard interval was always presented first in all tasks followed by the comparison interval.

4.2.3.1,1 Interval Comparison Task (pre/post training)

This task incorporated sixteen blocks, each consisting of 130 trials and employing 13 test intervals (35ms, 50ms, 71ms, 100ms, 141ms, 200ms, 283ms, 400ms, 566ms, 800ms, 1131ms, 1600ms, 2263ms) presented in a random order. The standard durations were each tested at ten comparison intervals (method of constant stimuli; standard multiplied by: 0.7, 0.86, 0.9, 0.94, 0.98, 1.02, 1.06, 1.1, 1.14, and 1.3). Sixteen repetitions per comparison interval were obtained with a total of 2080 trials across all sixteen blocks – one repetition of each test/standard in every block. Empty standard and comparison intervals (whereby the onset and offset of an interval is indicated by a beep) were presented to participants, who were required to indicate which interval was the longer one.

4.2.3.1.2.Rate Comparison Task

In this task, the standard and comparison segments were both two seconds in duration with a one second break in between. A series of beeps were phased in and out with a

Gaussian profile in order to make it difficult for participants if counting was attempted (rather than estimating the rate). The number of beeps presented in each segment was dependent on the rate (e.g. 100 ms ISI = 10 per second = 20 in 2 seconds) but participants couldn't actually hear the first few and last few (due to the Gaussian profile). For the standard, the interval between the beeps was 100ms and for the comparison the interval between the beeps ranged between 70ms and 130ms (ten variants: 0.7, .86, .9, .94, .98, 1.02, 1.06, 1.1, 1.14, 1.3 x standard) presented in a randomised order. One block, consisting of sixteen repetitions of each variant (160 trials) was completed both during the pre- and post-training stages. Participants used the left and right arrow keys (←, →) on a standard keyboard to indicate which segment of beeps was higher in rate (faster).

4.2.3.1.3. Line Comparison Task

This was a control task requiring visual length discrimination of two consecutively presented lines. Line presentation lasted 500ms followed by a one second break prior to the presentation of the comparison line. Two different standards were used; 200 and 400 pixels (in a random order) and ten different comparisons ranging from 0.7 to 1.3 times the length of the standard (also randomised; proportions as per rate comparison task), with sixteen trials per comparison (320 trials per block). To prevent participants judging line length based on position relative to the screen, the location of the line was randomly varied whereby one would appear 30 pixels to the left and one 30 pixels to the right of centre. Participants used the left and right arrow keys (←, →) to indicate which line they thought was longer.

4.2.3.1.4. Temporal Order Judgement (TOJ) Task

For the TOJ, two beeps were played from a left and right speaker – each left/right pair of beeps was played with a particular inter-stimulus interval, measured in milliseconds and

selected at random, out of a total sixteen possibilities, with negative values meaning the right beep occurred before the left: -200ms, -65ms, -55ms, -45ms, -35ms, -25ms, -15ms, -5ms, 5ms, 15ms, 25ms, 35ms, 45ms, 55ms, 65ms, 200ms. Each value was repeated fifteen times (240 trials). Participants were asked to indicate as to whether they heard the first beep from the left or right speaker by clicking the appropriate button on a mouse.

4.2.3.1.5. Reproduction Task

In this task target durations of either; 566ms, 800ms or 1131ms were presented in a random order. A hundred and fifty trials per block were completed (50 per target duration). The task required participants to complete an empty interval demarcated by two beeps, i.e. a second after the target interval presentation ended, the first beep was provided and the participant was required to press a button in time to match the target duration.

4.2.3.1.6. Tapping Task

The same target intervals that were used for the reproduction task (566ms, 800ms, 1131ms) were used for the tapping task. Nine trials, three for each target interval were completed. Participants used the hand pedal to tap along with a presented sequence of ten beeps and maintain the tapping rhythm across a continuation phase, comprising of twenty repetitions of each target interval (total of 60 taps per condition).

4.2.3.2 Training Stage

Fourteen sessions comprising of six to eight auditory interval discrimination blocks each were completed over a period of two months, totalling 96 blocks by the three main participants. In the context of the current chapter, these blocks acted only as training,

however data from these blocks were also analysed to test a different set of hypotheses to those addressed here (see Chapter 3). Eight of the durations used in the corresponding task from the pre- and post-training conditions were included in the training sessions; 71ms, 100ms, 141ms, 200ms, 400ms, 566ms, 800ms, 1131ms. Each block included one standard duration with 8 repetitions of 8 different comparison values: 0.86, 0.9, 0.94, 0.98, 1.02, 1.06, 1.1, and 1.14 x the standard, totalling 64 trials per block. As detailed in the discussion section, each standard interval block was completed before moving on to the next standard so as to maximise learning (Banai, Ortiz, Oppenheimer & Wright, 2010). Twelve blocks per standard duration amounted to 6144 trials (768 trials per standard; 96 repetitions at each comparison interval). Otherwise all details were as described in the pre- and post-training interval discrimination task, except that feedback ("correct" / "wrong") was presented after every trial.

4.2.4. Data Analysis

Transfer was assessed separately for each participant and task. For most tasks, a measure of the slope was obtained by applying a maximum-likelihood cumulative Gaussian fit to each duration in the pre- and post-practice sessions and estimating the SD of the underlying noise. Transfer of training was assessed by comparing pre- and post-interval training data by doing an inferential bootstrap test (by performing 4999 simulated resampling and fitting of the observed data) for the interval discrimination, TOJ, line comparison and rate tasks to obtain a 95% confidence interval on the difference in SD (yielding $p < 0.05$ when this interval did not include zero). For the tapping task, the raw data was detrended, by applying linear regression for each tapping block, from which a mean reproduced time and the standard deviation thereof was obtained. Values more than two standard deviations below or above the mean were removed. The squared difference of each trial from the mean reproduced value is a measure of the variable error and was

used in t-tests. The procedure for the motor reproduction task was similar although no detrending of the data was required.

RESULTS

4.3.1. Interval Discrimination

The initial data analysis revealed significant improvement on a few of the trained durations for the first two participants (P1 & P2). Better performance was observed mainly in the midrange (100ms, 200ms, 566ms) for P1 and P2. No improvement on any of the trained or untrained durations was observed for P3. Furthermore no pre/post comparison could be conducted on the highest duration due to a complete failure on the task and this value was therefore omitted from the graph and significance table. In order to confirm that the practice effects (and lack thereof) in the interval discrimination task is an accurate representation of training processes, correlation analysis to test the consistency of pre to post test scores for each participant was conducted. P1 and P2 were shown to have a high level of internal consistency, .99 and .98 respectively. This was not the case for the third participant who had a negative correlation of -.51 suggesting that the observed lack of training effects is likely due to individual differences, with this participant being unusually noisy. Figures 4.1 – 4.3 represent the pre- and post-performance for P1, P2 and P3.

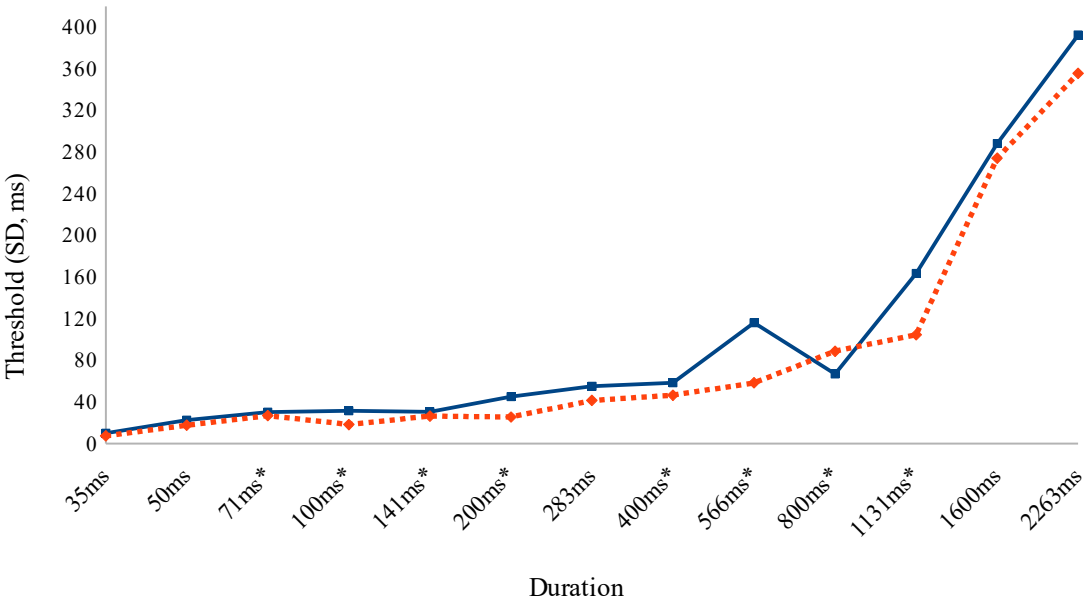

Figure 4.1. Pre- and post-test performance at all durations for P1. (Pre-test – solid line, Post-test – dashed line). Trained durations are marked with an asterisk.

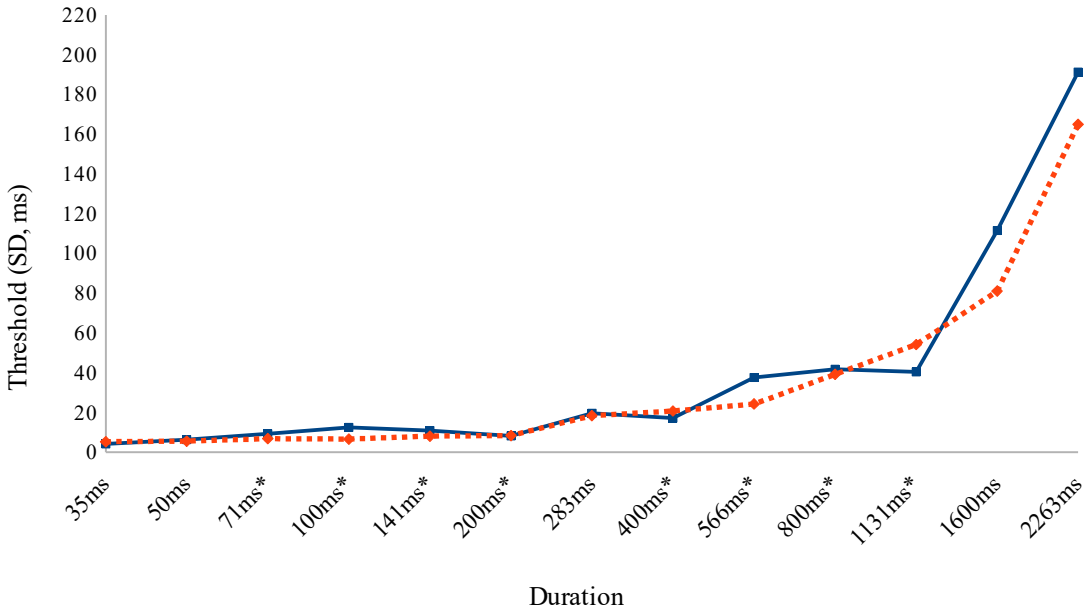

Figure 4.2. Pre- and post-test performance at all durations for P2. (Pre-test – solid line, Post-test – dashed line). Trained durations are marked with an asterisk.

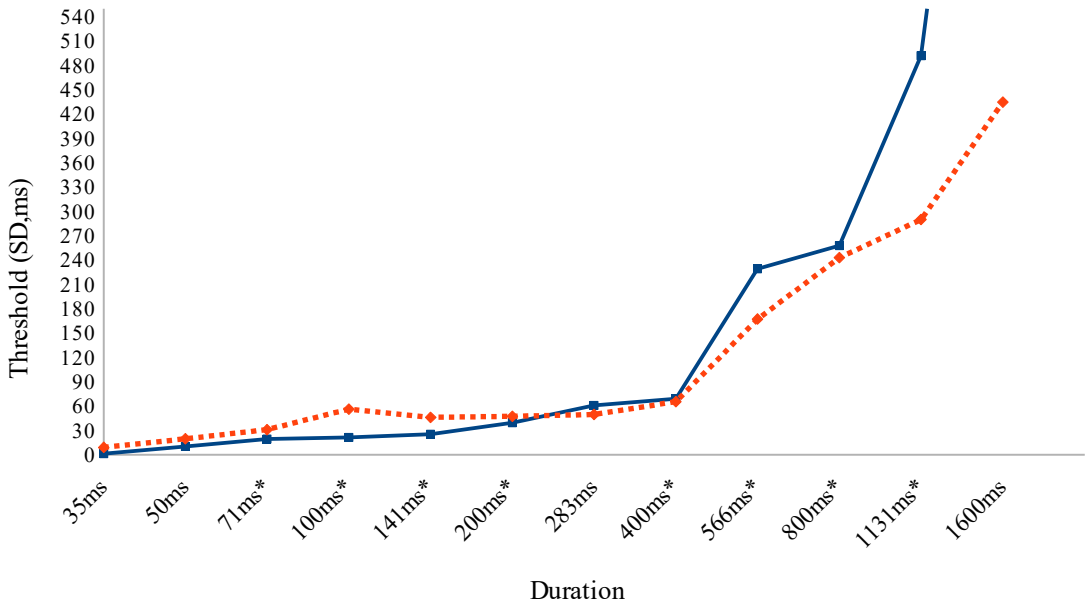

Figure 4.3. Pre- and post-test performance at all durations for P3. (Pre-test – solid line, Post-test – dashed line). Trained durations are marked with an asterisk The pre-test value of 1297 for the 1131ms duration is not included on the graph. As mentioned in the main text, a complete failure on the task was observed at the longest duration and was therefore omitted.

In addition to assessing improvements at each duration separately, the trained set of eight durations and the untrained set of five durations were re-expressed as Weber fractions and each considered collectively (for each participant separately) via repeated-measures t-tests. No significant overall effects were observed for the trained (or untrained) durations for P2 or P3. However P1 showed a significant improvement on both the trained (p= . 015) and untrained (p= .045) durations. Table 4.2 lists the statistical significance at each duration for all three participants.

Table 4.2. Details of pre- and post-practice results for each duration. Trained durations are noted in bold italics, statistically significant improvements in durations are marked with an asterisk. As mentioned in the main text a complete failure on the task was observed for P3 at the longest duration and was therefore omitted.

Duration	P1	P2	P3
35ms	p =.191	p = .162	p = .143
50ms	p =.293	p = .282	p = .354
71ms	p =.397	p = .077	p = .576
100ms	p = .027*	p = .004*	p = .397
141ms	p =.299	p = .126	p = .145
200ms	p = .018*	p = .505	p = .578
283ms	p = .142	p = .401	p = .479
400ms	p = .191	p = .292	p = .821
566ms	p = .024*	p = .046*	p = .366
800ms	p = .090	p = .375	p = .894
1131ms	p = .090	p = .197	p = .120
1600ms	p = .430	p = .123	p = .124
2263ms	p = .379	p = .244	—

4.3.2. Additional tasks

The results from the various additional tasks included as pre/post tests are shown in Tables 4.3 to 4.6. The most striking result that was observed was an improvement in the motor tasks (interval reproduction and tapping tasks) for the trained participants. Complete details for the participants (including controls) are presented in table 4.3 a-c and 4.4 a-c. No significant change was observed in the tapping task for the 566ms duration, at least for the trained participants. However, P3 displayed significant improvement on the 800ms tapping task, although no effect was noted for the other two participants, whilst the control subjects' performance actually deteriorated from pre- to post-test. In the 1131ms duration P1 and P3 showed significant improvement as did one

of the control participants (C2), although that may be accountable to the particularly weak performance observed in the pre-test.

Table 4.3 a-c Variable error for the Tapping task at the three trained durations, 566ms, 800ms & 1131ms for all participants. Statistically significant improvements in durations are marked with an asterisk.

a. Tapping Task – 566ms

		PRE TRAINING		POST TRAINING				
		M	SD	M	SD	df	t	p
Participants	P1	251.93	291.82	263.00	304.36	96	-.183	.855
	P2	92.04	97.27	141.51	148.14	100	-1.96	.052
	P3	303.89	374.788	273.42	332.73	103	.438	.663
Control	C1	1774.50	2311.94	2441.40	5001.33	113	-.920	.359
	C2	1909.62	2045.570	1156.02	1692.85	133	2.190	.030

b. Tapping Task – 800ms

		PRE TRAINING		POST TRAINING				
		M	SD	M	SD	df	t	p
Participants	P1	786.471	921.59	1117.17	1014.37	102	-1.812	.073
	P2	258.81	270.51	207.60	243.60	106	1.322	.189
	P3	1430.751	1514.81	348.59	412.59	90	4.29	.000*
Control	C1	1430.96	1966.73	5767.72	7831.633	112	-4.023	.000
	C2	1030.65	1203.75	1367.12	1427.16	153	-1.562	.120

c. Tapping Task – 1131ms

		PRE TRAINING		POST TRAINING				
		M	SD	M	SD	df	t	p
Participants	P1	4226.42	404.89	2389.99	2083.37	111	3.135	.010*
	P2	546.148	534.420	408.60	492.46	109	1.548	.125
	P3	2622.03	2734.04	1554.59	1926.88	104	2.185	.031*
Control	C1	1266.41	1567.92	2746.73	4046.13	112	-2.541	0.12
	C2	12823.3	18290.4	3498.16	3929.37	173	4.814	0.00*

In the interval reproduction task, no significant effects were observed for P1 and P2 in the 566ms duration, although improvement was noted for P3. All participants (P1, P2, P3) showed significant improvement in the 800ms and the 1131ms duration conditions (Table 4.4. a-c) while controls were inconsistent, showing one significant improvement but two significant drops in performance across this range.

Table 4.4 a-c Variable error for the interval reproduction task at the three trained durations, 566ms, 800ms & 1131ms for all participants. Statistically significant improvements in durations are marked with an asterisk.

a. Interval Reproduction Task – 566ms

		PRE TRAINING		POST TRAINING				
		M	SD	M	SD	df	t	p
Participants	P1	3549.45	4476.77	2712.69	3508.42	93	1.013	.312
	P2	392.70	511.63	459.33	595.85	92	-.581	.563
	P3	15978.3	33189.34	7903.1	12540.62	95	1.668	.013*
Control	C1	108620.	120796.5	55834.4	47638.9	97	-2.849	.005
	C2	7055.2	10863.96	13022.87	20560.86	97	-1.811	.073

b. Interval Reproduction Task – 800ms

		PRE TRAINING		POST TRAINING				
		M	SD	M	SD	df	t	p
Participants	P1	8018.80	10060.10	4410.373	5083.72	93	2.213	.031*
	P2	2206.59	2555.77	797.57	869.79	94	3.616	.006*
	P3	14484.32	23895.12	6427.25	9401.09	95	2.213	.033*
Control	C1	52429.04	73792.05	26611.58	37356.23	92	2.140	.035*
	C2	7198.36	8703.97	14285.15	16604.40	94	-2.619	.010

Interval Reproduction Task – 1131ms

		PRE TRAINING		POST TRAINING				
		M	SD	M	SD	df	t	p
Participants	P1	21130.87	29375.87	6171.06	7611.33	95	3.449	.001*
	P2	1617.40	1788.80	633.81	933.62	91	3.313	.001*
	P3	10180.78	13363.62	5539.95	7039.94	95	1.668	.036*
Control	C1	55307.59	75106.28	36629.43	34548.91	96	1.582	.117
	C2	3319.82	4044.34	10965.52	15180.80	92	-3.336	.001

Turning to the other temporal tasks, performance for P1 was noted to significantly improve on the TOJ task, but no improvement in either of the tasks (TOJ or rate) was noted for the remaining two participants and P2 actually became significantly worse at the TOJ (Table 4.5). No improvement in task performance was observed on the control task for any of the participants (Table 4.6).

Table 4.5. Pre and post training details for all participants for the rate and TOJ tasks. P values refer to changes in precision (here shown as SD).

	Rate						*TOJ*				
	PRE TRAINING		POST TRAINING				PRE TRAINING		POST TRAINING		
	PSE	SD	PSE	SD	p		PSE	SD	PSE	SD	p
P1	99.01	3.69	97.52	4.22	.237	P1	21.89	49.34	-0.047	20.51	.002*
P2	99.03	2.41	98.98	1.27	.077	P2	-3.254	20.31	-3.68	31.34	.020
P3	101.4	5.61	101.3	4.87	.058	P3	19.12	84.22	11.11	56.87	.114

Table 4.6. Pre and post training details for all participants for the line length control task. P values refer to changes in precision (here shown as SD)

	Line length (short)						*Line length (long)*				
	PRE TRAINING		POST TRAINING				PRE TRAINING		POST TRAINING		
	PSE	SD	PSE	SD	p		PSE	SD	PSE	SD	p
P1	203.0	13.59	198.5	14.60	.375	P1	416.4	37.96	418.3	34.51	.354
P2	198.3	10.51	195.7	12.10	.314	P2	412.1	14.85	419.1	19.21	.127
P3	189.8	16.38	195.3	16.33	.994	P3	402.7	30.34	386.7	29.07	.862

DISCUSSION

The current study aimed to assess the efficiency of perceptual learning for interval discrimination and the generalisation of any gains to untrained durations and temporal tasks. Training was observed to improve performance at a few of the practised durations for two of the participants, with a more global improvement for one participant. Participant 1 also showed a significant generalisation to untrained durations (when they were considered collectively), although participant 2 did not; echoing the inconsistent results for transfer to different durations described in the introduction (Lewis and Miall,2009). As already mentioned within the results section, the lack of stability in the pattern of thresholds across the pre- and post- trials for the third participant indicates that their performance was unusually noisy – it is therefore unlikely to provide a good account of the typical nature of generalisation across trained and untrained intervals, and is more likely attributable to individual differences and variable temporal sensitivity.

Generalisation to the motor tasks was observed consistently in two of the trained durations (800ms and 1131ms) for all three participants although improvement was more prominent in the interval reproduction task. Transfer on these tasks was inconsistent between the two control participants, and the control participant who showed a normal

level of baseline performance on these tasks (i.e. similar to the trained participants at pre-test) actually got worse at post-test. This would indicate that some transfer as a result of the training took place.

A speculative explanation for the improved performance in the motor tasks for the participants, who nonetheless didn't show significant improvements on the trained interval discrimination task, might be that certain tasks provide a more sensitive measure of time perception ability. Common behaviours relating to speech, movement and music for example, rely on the perception of temporal patterns, the sensitivity to which has been noticeable even in infancy (Hannon & Trehub, 2005). The tapping task relies on a 'beat', and synchronising one's movements to a regular time interval is said to require little conscious effort (Patel, Iversen, Chen & Repp, 2005). The reproduction task could similarly be noted to possess a rhythm whereby a potential strategy likening it to a beat might allow for better performance. A distinction between endogenous and exogenous mechanisms has been made in regards to the temporal orienting of attention which may further shed some light on the current results. With the latter, attention is involuntary and stimulus driven, in a sense automatic and relying on bottom-up processes whilst endogenous attention is more focus-driven and understood as a top-down process. Interval discrimination could therefore be said to require a more conscious effort than the two motor tasks used in the current study. Performance on tasks utilising endogenous and exogenous orienting was investigated by Rohenkohl, Coull who Nobre (2011) who found that performance was facilitated when a temporal rhythm was employed irrespective of whether participants directed their attention to the temporal structure of the task. This was not the case when the task had more symbolic cues. In order to achieve equivalent levels of performance, participants had to strategically focus on the stimulus and orient their attention to the temporal element. In the current experiment the level of allocated attention could therefore have introduced a bias whereby, irrespective of the temporal

learning which had taken place, performance in the task requiring less focus-driven attention may have shown better performance.

It could be argued that the observed transfer doesn't necessarily point to shared processes underlying motor and perceptual timing, and instead is an enhanced ability to store the learnt interval. However, this would apply more to the interval reproduction task. The tapping task on the other hand, could be regarded as a more implicit task and the data suggests that a certain amount of learning had taken place – a transfer from the interval discrimination task to the motor task points to shared or at least partially overlapping timing processes.

Interestingly, no generalisation was observed for the 566 ms duration. This duration specificity is in line with the proposal that distinct mechanisms underlie the processing of different durations and to a certain extent operate irrespective of modality and context (Nagarajan et al.,1998; Meegan et al., 2000; Bartolo and Merchant, 2009). However, the current data suggest that the long interval timing system is common across sensory and motor tasks (as transfer was observed at >=800 ms), whereas the short-interval timing system is more task specific (no transfer at 566 ms). The neural underpinnings of timing might therefore rely on an overlapping mechanism which would engage different cortical structures depending on the context. Neurons in the medial premotor cortex (of monkeys) were analysed in response to a series of interval reproduction and tapping tasks by Merchant, Pérez, Zarco, and Gámez (2013). The animals were trained on base durations (450ms, 650ms, 850ms, 1000ms) presented in blocked trials. Results from the tapping tasks revealed that the cells were tuned to specific durations with a considerable preference to the 850ms duration. This finding is comparable with the results of the current study where generalisation was noted for the two longest durations with no

significant effect in the 566ms duration, if we associate the premotor cortex with a longer-interval / general-purpose timing system.

Cross-modal transfer to an interval reproduction from an auditory interval discrimination task has previously been observed (Meegan et al, 2000). There, participants were trained on either a 300ms or a 500ms interval; participants who were in the 300ms training condition were noted to improve (in a comparison with the pre-test) on the 300ms interval reproduction task, whilst those in the 500ms displayed enhanced performance on the 500ms motor task. These findings were replicated using the same durations, albeit with somatosensory training as opposed to an interval discrimination task by Planetta & Servos (2008). The current experiment which again revealed cross-modal transfer at the trained durations further supports the notion that motor and perceptual timing likely rely on shared processes. It is interesting, however, that here the transfer occurred only at longer durations, and not at 566 ms, which was closest to the range where previous authors observed it. Imaging studies (Schubotz, Friederici & von Cramon, 2000; Coull, Nazarian & Vidal, 2008; Wiener, Turkeltaub & Coslett, 2010) have revealed certain commonalties in neural activation relating to motor and perceptual timing such as the ganglia-thalamo-cortical circuit which includes the medial premotor areas, presupplementary motor areas, the neostriatum, the globus pallidus and the motor thalamus. This system of neural pathways is also of particular relevance to a number of disorders (e.g. Silkis, 2001; Maia & Frank, 2017), which have been observed to display timing deficits in both motor and perceptual domains such as Parkinson's disease (e.g. Pastor, Artieda, Jahanshahi, Obeso, 1992; Piras, Piras, Ciullo, Danese, Caltagirone & Spalletta, 2014; Smith, Harper, Gittings, & Abernethy, 2007), Huntingdon's disease (e.g. Beste, Saft, Andrich, Müller, Gold & Falkenstein, 2007; Cope, Grube, Singh, Burn, & Griffiths,2014), Schizophrenia (e.g. Rammsayer, 1990; Davalos, Kisley & Ross, 2003; Carroll, Boggs, O'Donnell, Shekhar, & Hetrick, 2008) and ADHD (e.g. Rommelse,

Altink, Oosterlaan, Beem, Buschgens, Buitelaar, & Sergeant, 2008; Himpel, Banaschewski, Grüttner, Becker, Heise, Uebel, Albrecht, Rothenberger & Rammsayer, 2009; Rubia, Halari, Christakou, Taylor, 2009).

Reaction times and temporal order judgements have been suggested to rely on the same internal signal (Gibbon & Rutschmann, 1969; Cardoso-Leite, Gorea, & Mamassian, 2007) so if transfer of learning from an interval discrimination task to a motor task is observed, it could conceivably also enhance performance on a TOJ task. Studies comparing reaction times with temporal order judgements have often found that the two are affected differently by stimulus manipulations and more importantly stimulus duration (Jaśkowski, 1996), whereby the stimulus intensity has a greater effect on reaction times when compared to temporal order judgements (Jaśkowski, 1992; Javkowski & Verleger, 2000). However Miller and Schwarz (2006) suggest that these may simply be due to performance strategies in respect to differing task demands. In the present study the first participant was noted to show significant improvement on the TOJ task following the training phase, the third participant showed some improvement although the finding was not statistically significant, whilst the second participant displayed a significant decline in performance. It is possible that some shared components underlie these timing behaviours although on the basis of the current results no firm conclusion can be reached. No improvement on the rate task was observed for any of the participants which suggests that, most likely, distinct mechanisms govern the processes involved in these timing behaviours.

Transfer of learning has been observed to be influenced by a number of components. The amount of training, the training schedule and the utilised task itself could decide whether any benefits are passed on to other tasks or whether enhanced performance is strictly bound to the learned task (Ahissar & Hochstein, 1997; Green, Kattner, Siegel,

Kersten & Schrater, 2015; Larcombe, Kennard & Bridge, 2017). The extent of differences in task characteristics could be assumed to exert an influence on transfer to tasks which differ in modality or have different task requirements, but unless the mechanisms underlying different interval durations are distinct, it would be assumed that the above features would impose a negligible effect in the case of the current interval discrimination task. Another aspect which bears importance is that of individual differences and variations in timing, either due to the employment of different timing strategies or particular genotypes (Grahn & McAuley, 2009; Sysoeva, Tonevitsky & Wackermann, 2010).

Learning on a number of tasks can be facilitated or disrupted depending on the task schedule (Seitz, Yamagishi, Werner, Goda, Kawato, Watanabe, 2005; Tartaglia, Aberg & Herzog, 2009; Wright, Sabin, Zhang, Marrone & Fitzgerald, 2010; Szpiro, Wright, Carrasco, 2014). Alternating between different tasks during motor training has previously been observed to influence the level of transfer whereby blocked schedules usually promote lesser retention and transfer when compared to variable training (Shea & Morgan, 1979; Magill & Hall, 1990; Song, Sharma, Buch & Cohen, 2012; Lin, Chiang, Knowlton, Iacoboni, Udompholkul & Wu, 2013; Song, Gotts, Dayan & Cohen, 2015) although, as in the case of a motor study conducted by Müssgens & Ullén, (2015), this may pertain only to task-general rather than task-specific transfer.

These considerations might raise questions about the suitability of the training regime implemented here, in which the reference duration was blocked. However, gains in perceptual tasks have frequently been observed to correspond to learning specificity whereby learning may be specific to each task, although this can be dependent on the type of task itself, therefore it is often assumed that interleaving tasks would not improve transfer. This was demonstrated in studies which alternated between tasks (bisection and

Vernier discrimination) using the same stimulus and found no enhanced transfer in either (Huang et al., 2012; Li, Piëch, & Gilbert, 2004). Most critically for the current study, following training on an auditory interval discrimination task whereby participants either consecutively completed six blocks per duration (100ms & 350ms) or alternated between the two durations (after every two blocks) Banai, Ortiz, Oppenheimer & Wright (2010) found that learning took place in the consecutively-trained participants but not in the interleaved group. This observation directly informed our choice to train on one duration at a time in the current experiment.

Interestingly, transfer in the "consecutive standard" group of that experiment was found to generalise to untrained frequencies but not to untrained durations (Banai, Ortiz, Oppenheimer & Wright, 2010), consistent with the majority of studies looking at transfer across durations. In the current experiment participants completed blocks pertaining to each duration before moving on to the next, which in accordance with Banai et al. and the noted perceptual specificity, should yield more gains than interleaved practice. The current study likewise exceeded the suggested critical amount of practice per day for effective learning on an interval discrimination task (360 trials – Wright & Sabin, 2007), although the training was not on a daily schedule due to the number of trained durations and blocks. In terms of a training (rather than transfer) effect, the data obtained from the first and the second participant, in the interval discrimination task, is to a large extent congruent with previous studies. Transfer to other durations is less frequently observed; as already discussed in the introduction, the majority of studies (Rammsayer, 1994; Karmarkar & Buonomano, 2003; Wright et al, 2010; Bratzke at al. 2010), do not reveal transfer to untrained durations. The few studies which did observe a certain amount of transfer were usually noted to fall very close to the trained durations (Nagarajan et al., 1998; Bartolo & Merchant, 2009). Here, the evidence for transfer in Participant 1 was

driven mainly by the larger trends shown at very short durations, which are (at least in absolute terms) closer to the trained ones.

It must be emphasised that timing tasks are not simply a reflection of timing processes, as additional components must likewise be taken into consideration. For example, timing an interval requires holding that time estimate in memory in order to compare it to another interval. So one could ask whether the observed transfer of learning in timing is simply not due to an enhancement of a particular cognitive ability pertaining perhaps to improved encoding of a magnitude. The results of the line-comparison task within the current study seem to argue against this notion, as these processes would similarly be employed in this control task, yet no improvement for any of the participants was observed. This finding therefore allows for a dissociation between the temporal and non-temporal components relating to the transfer between the interval discrimination and the motor tasks. The current study design admittedly had some weaknesses whereby the control group consisted only of two additional participants, and they only completed a subset of tasks. Nonetheless it largely eliminates the possibility that improvements in performance on the motor tasks were due to any learning or strategy enhancement garnered during the pre-test stage by the other participants. The need for controls was only really necessary in the tasks which displayed some generalisation, which was most clear in the motor tasks.

Conclusions drawn from generalisation studies can further elaborate on the underlying mechanisms of interval timing. Contrasting models have been proposed, which can broadly be summed up to propose that timing either relies on a dedicated mechanism which functions across modalities and timing behaviours or depends on context-dependent models which imply that timing is inherent in neural dynamics, the so-called intrinsic models (e.g. Gibbon, Church, & Meck, 1984; Ivry & Schlerf 2008; Meck,

Penney, & Pouthas, 2008, Allman, Teki, Griffiths, & Meck, 2014). The current findings whereby improved performance was observed in only a subset of trained intervals, points to some temporal specificity which suggests that timing is governed by distinct mechanisms at different durations. Although the transfer to untrained durations observed in the current study for the first participant, might seem to indicate a common mechanism operating across long and short durations, it must be emphasised that training was undertaken in both these ranges, so it is only possible to assert that transfer to nearby durations can occur, but not necessarily across the supposed millisecond / second divide. Moreover, the transfer from perceptual to motor learning suggests a common mechanism underlying these timing behaviours. The results in which case can be reconciled by a third option whereby partially overlapping mechanisms with duration-specific circuits regulate interval timing processes (e.g. Buhusi & Meck, 2004; Nazarian & Vidal, 2008). Overall, perhaps the safest conclusion is that transfer of learning is a labour intensive method with which to assess commonalities across tasks, and perhaps for this reason is prone to generating somewhat inconclusive results. In the next chapter, an alternative method is adopted to address the same question.

CHAPTER 5 – IMPLICIT AND EXPLICIT TIMING

INTRODUCTION

Timing pervades all aspects of our existence; it is an essential element in action, language, and an important dimension of stimulus perception. In our day to day lives timing is required for a multitude of tasks; crossing the street for example, involves an indirect temporal component whereby the speed of an oncoming vehicle can be used to estimate when the vehicle will reach a given point and allow for a safe crossing (Lee, 1976). This type of timing, unlike an overt or an explicit estimation of time is considered to be implicit; here timing is a consequence of a non-temporal goal. Currently, the extent to which explicit and implicit timing tasks utilise a common timing system is unclear. As illustrated in the below figure (Figure 5.1), the distinction between implicit and explicit timing (with motor and perceptual timing allocated within each) has been reviewed by Coull and Nobre (2008) and it is in this context that the battery of tasks introduced in this chapter is organised.

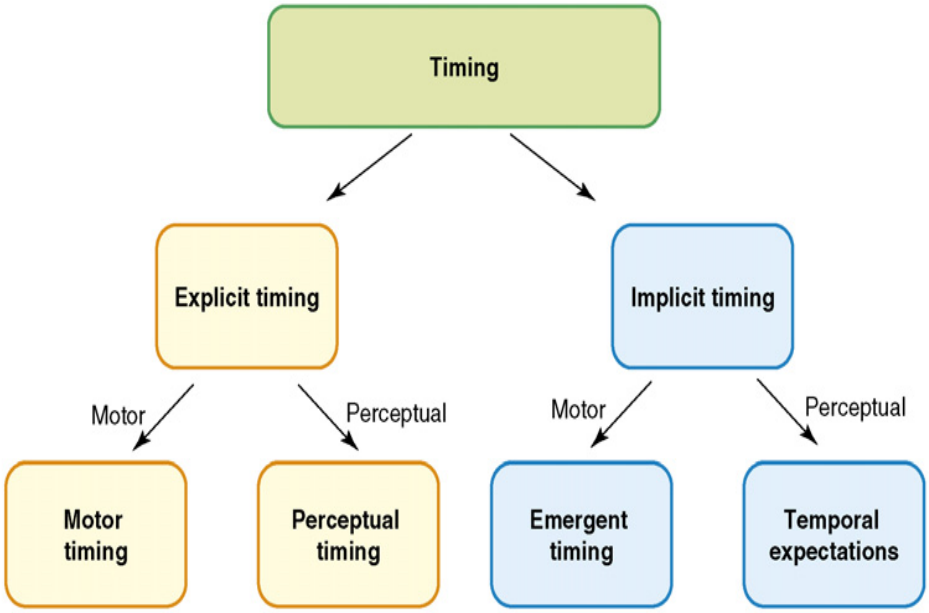

Figure 5.1. Dissociating explicit timing from temporal expectation with fMRI, Coull J.T & Nobre A.C. (2008) Current Opinion in Neurobiology, vol 8, pg 138. Reproduced with permission.

In addition to the explicit and implicit divide, a further segregation has been discussed within the implicit-timing domain. Implicit motor timing is said to refer to an emergent form of timing whereby as in the above real-life example, the speed of the vehicle allows for a prediction of its eventual location and from there allows for the appropriate action. By contrast, in implicit perceptual timing, temporal expectation is established and this is based on an expectation as to when a particular stimulus will appear. This can be a conscious estimation (endogenous) or a subconscious expectation (exogenous).

The definitions of the two main forms of timing as set out by Coull and Nobre, to a certain extent overlap with the cognitively controlled and automatic timing distinction, as discussed by Lewis and Miall (2003.b). Automatic timing here is noted to refer to an uninterrupted or continuous measurement of sub-second intervals based on motor timing, not requiring any attentional control whilst controlled timing recruits attention and is associated with supra-second estimates. However, as noted by Coull and Nobre, it is possible to time sub-second intervals in an explicit manner.

Traditional models suggest that timing is mediated by a dedicated amodal mechanism whereby all timing behaviours are coordinated by a single temporal mechanism. However, many behaviours contain a temporal component, and the range of tasks that might be considered to represent implicit timing is large. In this chapter, in addition to explicit and implicit timing tasks already considered within the time perception literature, an under-investigated form of timing – that of timing in language – is also investigated. Implicit timing is an essential component in accurate communication and so a novel task, in addition to amended versions of already existing language experiments, was created in order to analyse timing in language and to assess the possible commonalities within the different forms of timing that have previously been considered.

To summarise so far – while classic internal clock accounts suggest that a single system underlies many time-dependent behaviours, several authors have suggested a partial or complete dissociation between timing systems, for example for implicit and explicit timing. One way to assess commonalities is to seek correlations in the ability of participants to perform different timing tasks. Several such studies have been conducted, although the majority have tended not to focus on explicit/implicit distinction. Of those that do, some of them have used tapping and circle drawing tasks (which could be said to loosely map onto the implicit/explicit divide) although the noted lack of correlation could also be due to the difference in task demands as well as the joints which were used (mainly elbow and shoulder) to perform the movements. (Keele, Nicolletti, Ivry & Pokorny, 1985; Ivry & Hazeltine, 1995; Robertson, Zelaznik, Lantero, Bojczyk, Spencer, Doffin, & Schmidt, 1999; Rammsayer & Brandler, 2004; Ivry & Schlerf, 2008; Piras & Coull, 2011; Coull; Davranche, Nazarian & Vidal, 2013).

Other studies have included the implicit/explicit distinction within a larger battery of timing tasks. Multidimensional scaling, an analysis which reveals the underlying similarities in a large dataset, was applied to a dissimilarity matrix by Merchant, Zarco, Bartolo and Prado (2008) in order to investigate the relationship between ten timing tasks. The authors suggest that any noted performance variability can be viewed as an indicator of the neural mechanisms which are employed in the timing behaviours. All of the tasks were in the same interval range (350ms -1000ms) and were grouped into explicit/implicit, motor/perceptual visual/auditory and single/multiple interval tasks. The distinction between the number of timed intervals as well as the explicit and implicit tasks was deemed more significant than the noted differences in task modality. Participants relied on the wrist as the main drawing joint in both the circle and tapping tasks in this experiment, but similarly to the above noted studies no correlation between these timing tasks was observed.

In this chapter, I attempt something broadly similar to the study of Merchant et al., but with a particular focus on linguistic and very short-interval timing tasks. In the remainder of the introduction, some background will be provided for the more novel procedures within a battery of tasks intended to investigate correlations across implicit and explicit perceptual and motor timing systems.

5.1.1. Timing In Language

The importance of timing in speech has been emphasised in a number of psychoacoustical studies (reviewed by; Moore & Glasberg, 1986, Rosen & Fourcin, 1986), where it is noted that place-frequency mechanisms (as described in the two theories of hearing; The Place theory and the Frequency Theory) are not able to fully account for the perception of pitch and intonation in speech. Models of accurate speech perception state that time information is a significant component in human perceptual ability (Assmann & Summerfiled, 1990). Earlier studies conducted with patients with single-channel cochlear implants (which function by transforming acoustic vibrations into electrical stimuli and therefore do not allow for place-based frequency analysis), found that patients were able to understand speech segments based on the auditory signal alone, (Hochmair-Desoyer, Hochmair, Fischer, Burian, 1980) leading to inferences about the required level of temporal information required for accurate speech discrimination. This led to experiments with normal hearing participants in order to evaluate the significance of temporal elements in accurate speech perception (Van Tassel, Soli, Kirby, Widin, 1987; Rosen, Walliker, Brimacombe, Edgerton, 1989). Lesions studies with injuries to the auditory nerve (said to affect the temporal coherence of the discharges of auditory nerve fibres) were found to significantly impair speech perception highlighting the importance of temporal coding (Moller & Moller, 1985). These observations have added to the recent

developments in cochlear implants whereby coding for a higher temporal resolution has improved the speech discrimination of patients. (Moller, 1999; Rubinstein, 2004).

Multiple timescales are noted to underlie the systemic organisation of speech (Moore & Glasberg, 1986, Rosen & Fourcin, 1986). Notably the key temporal elements, based on dominant fluctuation rates (changes in the vocal output) are described as; the envelope (the 'temporal information' component which is referred to in much of the literature and includes features such as intensity, duration as well as rise and fall time; Rosen, 1992), periodicity (speech fluctuations between 50 and 500Hz) and fine structure (variations in wave shape). The acoustic features of the first component (i.e. envelope) relay linguistic information in the form of segmental cues to the manner of articulation, voicing[3], vowel identity and prosody. Fluctuations in periodicity correspond to fluctuations in frequency and further reveal linguistic elements pertaining to voicing and manner as well as intonation and stress. Finally the fine structure corresponds to the timbre, and in addition to providing segmental cues to voicing and manner also presents cues indicating the place of articulation and vowel quality (Rosen, 1992).

Due to the multitude of variations between different speakers, it has also been suggested that accurate speech perception relies on multi-resolution processing. Poeppel, Idsardi and van Wassenhove (2008) note that perceptual speech analysis occurs simultaneously on a range of 20 – 80ms, corresponding to sub-segmental and segmental speech sounds whilst the 150 – 300ms range reflects the syllabic and supra-segmental components. The latter coincides with the envelope of the sound waveform.

5.1.1.1Temporary sentence ambiguity – An implicit perceptual timing task

The different elements which make up speech correspond to different timescales, and

3 Speech sounds, particularly referring to consonants, which are either voiced or voiceless, such as the difference between p and b, the former being an example of voiceless and the latter considered as voiced.

spectral changes in the duration of a particular segment[4] can potentially alter the semantic meaning of the message. Likewise it has been noted that speakers tend to lengthen particular speech segments prior to a pause and these can in turn affect the conveyed message (Esposito & Bourbakis, 2006).

For this chapter, a task was sought that could be used to assess the precision with which participants encode the temporal information that informs our interpretation of language. To this end, phrase final lengthening was manipulated in an implicit perceptual language task, in order to introduce a so-called temporary ambiguity whereby the intended structure is revealed before the end of the sentence.

Two variants of a sentence with an identical onset up till the target word were used in the current experiment, and three speakers were asked to naturally read each of these sentences. The first sentence has a pause, as implied by a comma directly after the target word (shown in bold, below) resulting in an extended duration when compared to the duration of the word in the non-pause sentence variant.

The presence of this comma implies just one of the two possible sentence endings (underlined, below):

*When the tractor **pulls**, the rope <u>is stretched tight</u>.*

vs

*When the tractor **pulls** the rope<u>, the tree crashes down</u>.*

The duration of the target word, specifically the vowel and the subsequent voiced coda consonants, i.e. ull in p**ull**s, was manipulated so as to extend the non-pause variant towards the length of the pause variant and vice versa (see Figure 3.2 in the method

4 Vowels and consonants can be distinguished by spectral changes over tens of milliseconds, syllables by sequences of phonemes over a few hundred milliseconds, and the intonational contours of phrases and sentences by pitch variation over hundreds to thousands of milliseconds" (Overath et al, 2015)

section). Other variables (e.g. pitch) which could serve as a cue aiding selection were held constant. In the task, participants heard the first part of the sentence containing one of the ten possible target word durations and then chose the most befitting sentence ending. It was hoped that participants would select the correct sentence ending based on the target word duration, with ambiguous durations yielding a psychometric function which would allow for a measure of precision to be extracted.

5.1.1.2.Phoneme closure duration discrimination – A short-duration implicit perceptual timing task

Voice onset time (VOT) is a phonetic feature in the production of plosives; it is the time between when the stop is released and when the voicing of the following vowel begins. In other words it is the duration between the consonant start and the start of the vocal tract vibration. The consonants b and p are generated in a manner which doesn't allow for the vocal cord folds to vibrate until the release of the stop closure. The duration of the closure interval therefore corresponds to how plosives in certain English words are perceived. It has been observed that vowels are generally shorter before voiceless stops then they are before voiced ones (Lisker, 1974).

Differentiating between words such as rabid and rapid for example, without additional context has been found to rely specifically on timing cues (Lisker, 1957; Port 1977). Bilabial stops are consonantal sounds. The longer closures, e.g. the p in ra**p**id, is heard as voiceless whilst the shorter ones, the b in ra**b**id as voiced. Speech tempo has also been found to alter the perceived duration of the VOT (Gaitenby 1965) although other studies indicate that there is in fact a perceptual temporal boundary between the voiced and voiceless bilabial stops (Lisker, 1957; Port, 1978).

More recent studies (e.g. Esposito & Bourbakis, 2009) have provided further confirmation that the duration of a phoneme can act as cue to the phoneme itself (e.g. the perceptual distinction between latter and ladder depends purely on duration) and so will permit accurate discrimination without the aid of further contextual cues. The intervocalic difference in the two words used for the purpose of this particular experiment, mainly stems from the medial VOT. This is the time from when the voicing of the vowel begins to the burst of the consonant which can be positive or negative. For the purpose of the second language task (looking at durations below 80ms) the voicing of the medial stop in the words rabid and rapid was controlled by changing the duration of the stop closure or the stop period (also known as a plosive). This period was completely removed and then almost infinitesimal segments were inserted in order to expand the phoneme without a voiced vowel. Within "rabid", cuts were made immediately after closure for the medial b and just before the release. The glottal pulsing during the closure was discarded and silent gaps in 10ms steps ranging from 0ms to 80ms were inserted (short stop closures correspond to rabid whilst long closures to rapid) Participants listened to all steps and were required to state whether they heard rapid or rabid. The transition between the two words was noted to take place around 30ms so starting with short closures we hear rabid and progress to rapid with long closures.

At present, as far as I am aware, no other studies have explored the link between timing in language and other forms of timing and so that is a key aspect in the following experiment. These novel language timing tasks were used to represent the implicit perceptual branch of Coull & Nobre's (2008) proposed double bifurcation of timing systems. Several more standard timing tasks were included for comparison to represent the other branches. These included explicit perceptual timing tasks addressing various sub-second timescales, such as empty interval discriminations and temporal order judgements, as well an explicit motor timing task (temporal reproduction) and an implicit

motor timing task (temporal trajectory interception). All tasks yielded measures of temporal precision. The key prediction was that precision should correlate across tasks to the extent that they access a common timing system.

METHOD

5.2.1. Participants

A total of 61 volunteers agreed to take part in the current experiment, 16 of those were male and 45 female. Due to the amount of tasks that participants were required to complete, the experiment was divided into two sessions, and the order in which the tasks were completed was randomised. Twelve participants did not return to complete the second part of the experiment and were therefore not included in the analysis. Nine participants were further excluded due to a negative slope for tasks where a psychometric function was fitted or where the point of subjective equality was not within the range of tested values. The final number of participants included in the analysis was 40; 10 male and 30 female. All participants had normal hearing and normal or corrected to normal vision. The age range was between 18 and 44 (mean age: 23) All participants were provided with specific instructions prior to each task and were given the opportunity to complete practice trials. No feedback was given on any of the experimental trials.

5.2.2. Apparatus and Stimuli

The battery of tasks were run on a PC (connected to a Samsung SyncMaster 1100MB CRT monitor, able to provide a refresh rate of 100 Hz) running on a Windows XP operating system. Viewing position was maintained using a headrest. Further details particular to each task are detailed in the following sections.

5.2.3. Data Analysis

Even if a timing system provides a mean perceived duration that is close to target over a series of trials, the system may be poor. It might provide a correct mean response, but the variability of information might be high, with estimates being sometimes much briefer or much longer than those in real time. In other words, in many studies, it is not the mean estimates of the system that are of interest, but its capacity to minimize variability over trials (see Grondin, 2001b).In order to evaluate the commonality of timing processes, analysis here focused on the variability of responses rather than the point of subjective equality (PSE).

Psignifit, a Matlab toolbox (Wichmann & Hill, 2001) was used in order to achieve maximum-likelihood fitting and bootstrapping of data whenever a psychometric function could be used to model the range of probabilities of reporting one stimulus category as duration is varied, and thus provide an approximation of the discrimination threshold. In all cases, the psychometric function was assumed to be a cumulative Gaussian, and the threshold was calculated as the difference between the 84% and 50% values. This procedure was utilised for the following tasks: temporal order judgement (TOJ), interaural time difference (ITD), line comparison, temporary sentence ambiguity and phoneme closure duration discrimination.

The standard deviation of the reproduced intervals in the motor reproduction task and responses made in the spatio-temporal trajectory task was determined in Excel, after excluding any extreme outlying responses (> 2.5 x SD from mean).

Finally the d-prime (d') measure of sensitivity was used for the flutter detection task. This was calculated using signal detection theory which attributes responses to a combination

of sensitivity and bias (Green & Swets, 1966). Single interval detection was employed to avoid response bias, and both correct detections and false alarms were taken into account. The task provides a measure equivalent to slope / SD measure of other tasks in the battery, but with reversed sign (i.e. high d' = small SD).

5.2.4. Design and Procedure

5.2.4.1.Duration discrimination tasks

A. Stimuli and apparatus

The experiment was controlled by a PC sending digitised signals at 44100 Hz using a 12 bit A/D card (National Instruments DAQCard 6715). A standard USB computer mouse was used to record judgements. Auditory stimuli were delivered via digitised signals at 44100Hz. Experimental software was programmed in-house using C++. A 10ms 1000 Hz tone was used to denote the onset and offset of each empty interval. Two standard interval durations were used, 50ms and 360ms, to distinguish the two tasks. These durations were selected as an approximate match to the intervals spanned by our language task manipulations (see below). In both the short (50ms) and the long (360ms) interval discrimination task, the comparison interval was 0.73 to 1.27 of the duration of the standard (in 10 steps of 0.06). So the comparison interval for the former ranged from 37ms to 64ms whilst the latter range was from 263ms to 457ms.

B. Procedure

A well-known and traditional method of investigation, the interval discrimination task using an empty interval was incorporated in the battery of tasks. Participants completed one block in each task (50 vs 360ms) with every block consisting of 80 trials (8 at each comparison interval). The standard interval was presented first followed by the

comparison interval. The inter-stimulus break between the two intervals was set at 1000ms. After each auditory presentation, a dialog box would appear on the screen asking which interval was estimated to be longer, the first or the second. The participant then initiated the start of the next trial by making their response.

5.2.4.2.Motor reproduction task

A.Stimuli and apparatus

Data was recorded with a precision to one millisecond, using a twelve-bit DAQPad 6015 A/D card (National Instruments) connecting the computer to a digital switch, in the form of a hand pedal. The experiment was controlled by a PC sending digitised signals at 44100 Hz using a 12 bit A/D card (National Instruments DAQCard 6715). As with the above tasks, experimental software was programmed in-house using C++. A 10ms 1000 Hz beep was used to denote the onset and offset of each empty interval. Three durations were tested; 360ms, 720ms and1080ms. The interstimulus break was 1000ms.

B. Procedure

A commonly used procedure utilised in timing literature – an interval reproduction task was employed for the explicit motor aspect of the experiment. Participants were presented with an empty interval and were required to reproduce the duration by pressing a hand pedal, i.e. Two beeps were presented by the computer, one to indicate the onset and the next the interval offset, followed by a pause, then a third beep to start the reproduction interval which the participant would then end with a press of the pedal. Participants completed one block of 120 trials, with 40 trials with each duration intermixed randomly.

5.2.4.3. Spatio-temporal trajectory

A. Stimuli and apparatus

Experimental software was programmed in-house using C++. Responses were recorded via a digital button/DAQPad, as per the reproduction task.

B. Procedure

The implicit motor task conducted in the current experiment was a spatio-temporal trajectory task whereby the stimulus (a small black filled circle; 10 pixel diameter, approximately 0.4 degrees visual angle) travelled in a straight horizontal path at a particular constant velocity. Participants were required to respond (by pressing a button on the hand pedal) when the moving stimulus reached its destination (a vertical red line intersecting the screen at its midpoint). Three conditions or durations were included – a fast (360ms) medium (720ms) and slow (1080ms) speed. Different speeds/durations were randomly intermixed. Circles always began at the same fixed position to the left of the screen. Prior to each trial the stimulus would flash one to three times in a manner corresponding to the speed at which it would travel, a cue to alert the participant and allow for an adjustment of expectation. Each trial would start automatically one second after the participant's previous response. Participants completed a single block consisting of 120 trials, 40 per duration.

5.2.4.4.Temporal order judgement task (TOJ)

A. Stimuli and apparatus

A standard USB computer mouse was used to record judgements. Auditory stimuli were 10 ms 1000 Hz pure tones delivered via digitised signals sent through a twelve-bit A/D

card (DAQCard 6715; National Instruments). Experimental software was programmed in-house using C++. A standard USB computer mouse and keyboard were used to record judgements. Participants listened to the auditory beeps on two small speakers placed at the left/right hand base of the headrest. Sixteen variations of these were played to the left and right ear, the inter-stimulus intervals ranging from -200ms to 200ms and presented at random (Right side first; -200, -65, -55, -45, -35, -25, -15, -5, Left side first; 5, 15, 25, 35, 45, 55, 65, 200ms). Five repetitions of each value, totalling 80 trials were completed.

B. Procedure

Experiments investigating TOJ focus on the magnitude of the interval between two presented stimuli, aiming to establish the required duration for the two events to be perceived as separate and to accurately gauge the presented order. The participants were required to decide whether the stimulus was presented to the right or left ear first. After each stimulus presentation, a dialog box would appear on the screen asking which beep was heard first; left or right. The following trials were initiated with a mouse click.

5.2.4.5.Interaural Time Difference (ITD)

A. Stimuli and apparatus

Participants used Sennheiser PX360 headphones for this task. Programming was done in Matlab with the Cogent 2000 toolbox (http://www.vislab.ucl.ac.uk/cogent_2000.php). A 500 Hz sine wave was played to both ears with one slightly out of phase with the other. The phase differences (ITD's) ranged from -500 μs to 500μs. A triangular window was applied at the start/end of the one second stimulus duration so that the sound ramped up over the first 250ms and faded out over the last 250ms.

B. Procedure

One stimulus presentation per trial (method of single stimulus) was completed by the participants with 8 trials at each of the 11 possible ITD's randomly intermixed in a single block. The participants were required to decide whether the stimulus appeared to come from the left or right. After each stimulus presentation an onscreen message required the participant to press a key on the computer keyboard (A for left and L for right).

5.2.4.6.Auditory flutter-fusion task

A. Stimuli and apparatus

Apparatus was as for the TOJ task above. The flutter was amplitude-modulated (AM) white noise with an AM frequency of 200Hz (a typical threshold for detecting flutter with a medium modulation depth). The signal amplitude averaged 1.0 arbitrary units but reached peaks and troughs 0.4 units above and below this average. The signal was produced by a DAQCard 6715 A/D card, digitised at 88200 Hz.

B. Procedure

One block consisting of 40 trials with flutter and 40 trials without, was presented to participants. The no signal trials consisted of AM white noise modulated at 5000Hz (although not strictly the absence of flutter, this is well above threshold, and, importantly contains the same average signal intensity as the target stimulus). After each trial, the participants' task was to indicate whether they perceived the stimuli to have a 'flutter' or not by using the appropriate arrow key on the keyboard. As in the above tasks this question was presented visually on the computer screen after each auditory presentation.

5.2.4.7.Line comparison task – Control task

A. Stimuli and apparatus

Experimental software was programmed in-house using C++. A standard keyboard was used to record judgements. A comparison line was first shown on the screen for a duration of 500ms, followed by the standard line (200 pixels, with an approximate visual angle of 8 degrees) after a one second break. Ten different comparisons were used, starting with 0.8, then 0.93 to 1.07 in 0.02 steps, and then 1.2 times the length of the standard. A random jitter was applied to the lines, i.e. one was moved 30 pixels to the left and one moved 30 pixels to the right so as to prevent participants relying on line end position rather than line length in their judgements.

B. Procedure

Participants were presented with the comparison line, after which the standard line would appear. The participants' task was to indicate which line was the longer using the left and right arrow keys.

5.2.4.8.Temporary sentence ambiguity

A. Stimuli and apparatus

Experimental software was programmed using Matlab with the Cogent toolbox. A standard computer keyboard was used to record judgements. Two variants of a sentence with an identical onset up till the target word were used, as detailed above in the introduction. The duration of the vowel and the subsequent voiced coda consonants was manipulated in a calculated gradient (six equal steps) with Praat software so as to extend

the non-pause variant to the length of the pause variant (Figure 5.2a and 5.2b). Three speakers were used, with the durations detailed below:

When the tractor pulls, the rope is stretched tight

(target word, *'pulls'* duration: speaker 1 – 0.485s, speaker 2 – 0.468s, speaker 3 – 0.389s)

When the tractor pulls the rope, the tree crashes down

(target word, *'pulls'* duration: speaker 1 – 0.248s, speaker 2 – 0.265s, speaker 3 – 0.282)

Sentence Var. 1 mean: 467ms

Sentence Var. 2 mean: 265ms

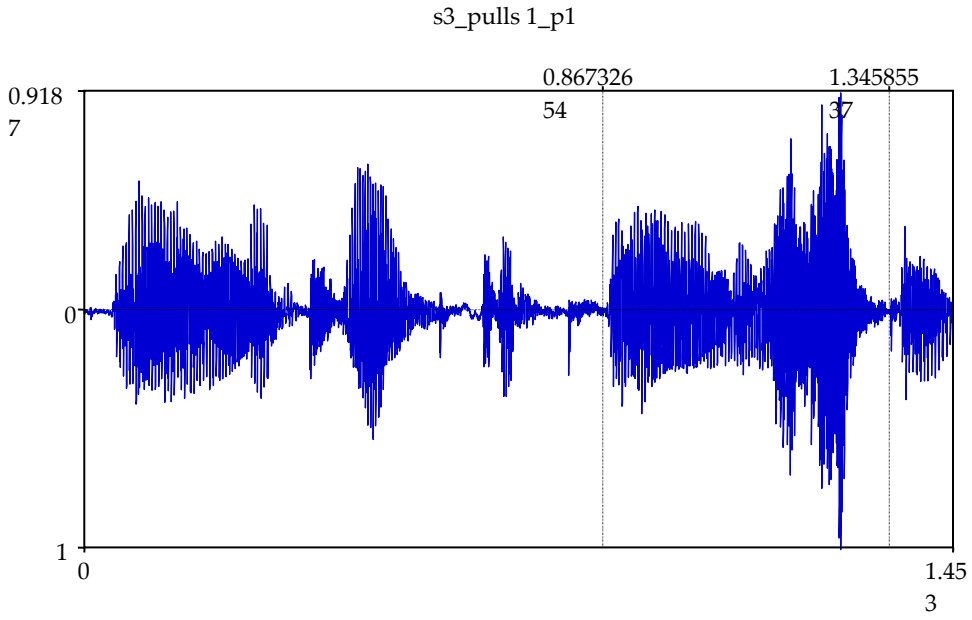

Figure 5.2a The original pause variant. Time given in ms.

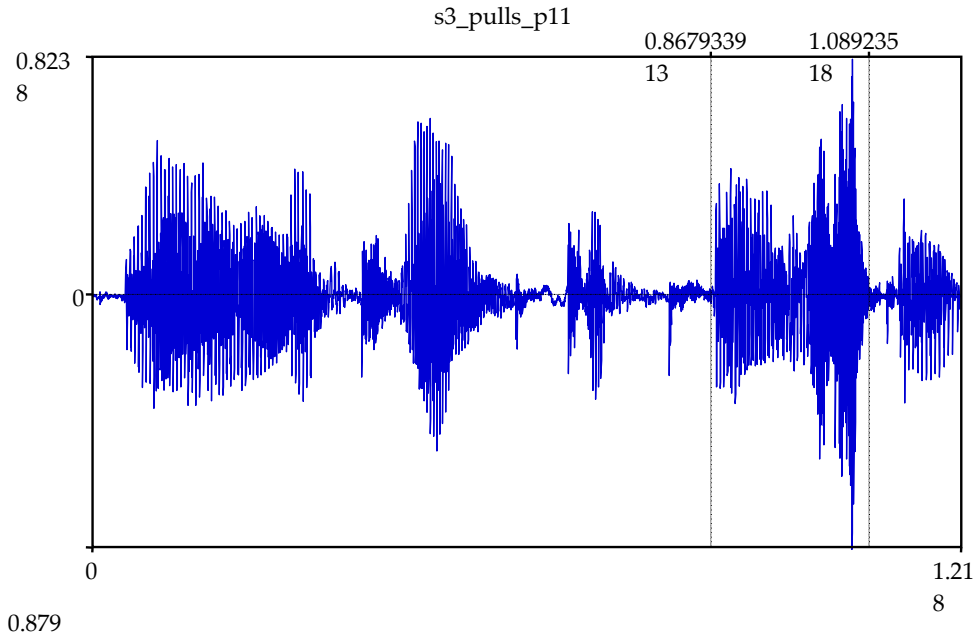

Figure 5.2b The original pause variant (in this instance, speaker 3) as depicted in 5.2a which after a number of gradual steps, i.e.1 to 11 cuts (as detailed in the method section), has been shortened, 5.2b, to match the duration of the non-pause variant. Time given in ms.

B. Procedure

Participants were first required to listen to the two complete sentences a minimum of five times. In the task they were presented with the first part of the sentence; "When the tractor pulls" and asked to complete it with what they thought was the most befitting ending. The two endings would appear on screen and participants were required to press either the A or L key on the computer keyboard depending on their sentence ending selection. Sixty repetitions of the sentence in each block (3 blocks, each corresponding to one of the 3 speakers) were presented with 6 possible variations (differing target word durations) each repeated 10 times. It was hoped that participants would select the correct sentence ending based on the target word duration, and when the duration was ambiguous internal noise would yield a psychometric function from which a measure of precision

could be extracted. The psychometric function was fitted separately for each speaker and an average slope from successful fits was obtained.

5.2.4.9.Phoneme closure duration discrimination

A. Stimuli and apparatus

Experimental software was programmed using Matlab with the Cogent toolbox. A standard computer keyboard was used to record judgements. As in the above experiment, multiple speakers were used, but in this case just two. Praat software was used to manipulate the duration of the stop closure in rapid/rabid by first cutting the stop period completely and then reinserting it in 10ms steps from 0 to 60ms. The below figures (figure 5.3a and 5.3b) illustrate the ra**b**id to ra**p**id transition.

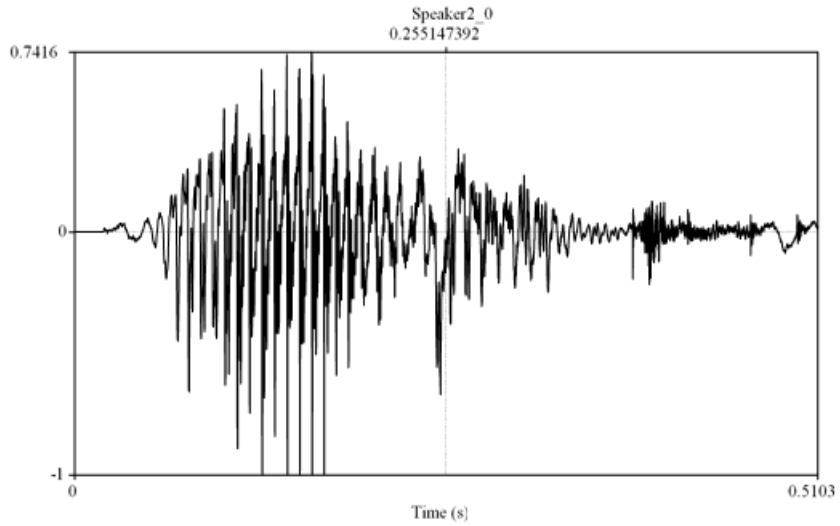

Figure 5.3a 'Rabid' voice pattern (speaker 2) prior to any manipulation.

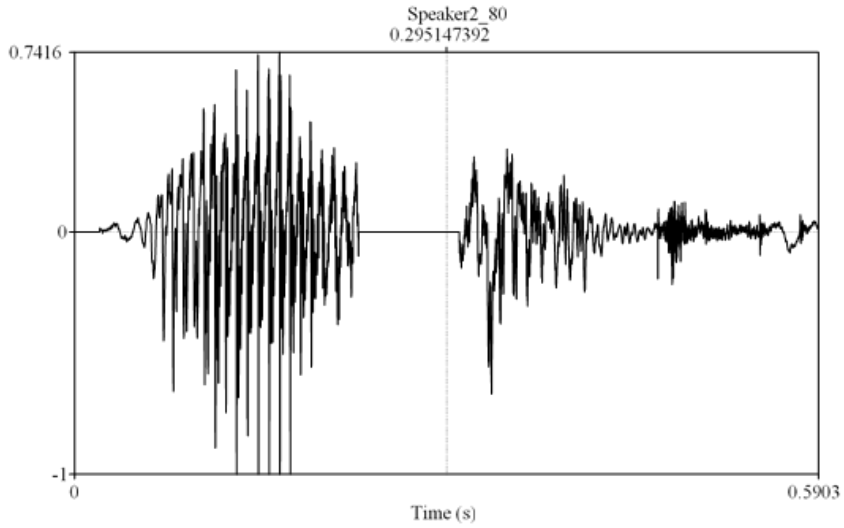

***Figure** 5*.3b Manipulated voice pattern (speaker 2) - rapid

B. Procedure

Participants were presented with all 7 variations from each speaker, 10 repetitions of each, with a total of 140 trials randomly allocated in a single block. They were once again required to indicate their selection (rabid/rapid) by pressing either the A or L key on the computer keyboard.

RESULTS

This experiment sought to investigate the possible commonalities in the underlying mechanisms of various timing behaviours. Exploratory factor analysis (EFA), an analytical method which reduces the dimensionality of a data set and estimates any interdependence between variables was initially employed (Bartholomew, Knott, & Moustaki, 2011). As a general rule of thumb it has previously been suggested that sample

size or sample to variable ratio is a key aspect of consideration when conducting factor analysis. However, it has also been argued that considerations pertaining to specifics of the study design and dataset (MacCallum, Widaman, Zhang, & Hong, 1999; Preacher & MacCallum, 2002) could allow for its efficient utilisation on smaller samples, like the one obtained here. Prior to EFA, a log10 transformation was applied to reduce skew in the data (with the exception of the 'flutter' task). The influence of a shared factor(s) on the various temporal behaviours (factor loading) was estimated using the Maximum Likelihood method (ML), a fitting procedure commonly used in EFA. The descriptive statistics for all tasks are reported in Table 5.1.

Table 5.1 (Log10) mean task performance on 13 timing and 1control tasks. Int = duration discrimination, Ball = moving ball task, Rep = duration reproduction, TOJ = Temporal order judgement, R-R = Rapid/Rabid discrimination language task, Pulls = 'Pulls' language task, ITD = Interaural time difference, Flutter = Amplitude modulation task. *units of seconds, not milliseconds as in other timing tasks **Not log transformed.

TASK	TYPE	PERFORMANCE MEASURE	MEAN	SD
360 + ms				
Int 360	Explicit /Perceptual	Response variability	1.60	.258
Ball 360	Implicit/Motor	Response variability	1.59	.138
Ball 720	Implicit/Motor	Response variability	1.55	.239
Ball 1080	Implicit/Motor	Response variability	1.55	.228
Rep360	Explicit/Motor	Response variability	1.98	.278
Rep 720	Explicit/Motor	Response variability	2.04	.223
Rep 1080	Explicit/Motor	Response variability	2.01	.269
~50 ms				
Int 50	Explicit /Perceptual	Response variability	1.31	.405
TOJ	Explicit/Perceptual	Difference Limen	1.75	.455
R-R	Implicit /Language	Difference Limen	1.08	.336
Pulls	Implicit /Language	Difference Limen	-1.36*	.591
Higher resolution timing				
ITD (μs)	Implicit /Perceptual	Difference Limen	2.28	.352
Flutter (d')	Implicit /Perceptual	d'prime sensitivity	1.77**	1.451

The Kaiser-Meyer-Olkin (KMO) statistic is a measure of sample adequacy for each variable as well as the complete model. For a sample to be considered adequate a KMO greater than 0.5 is required. In the current experiment a KMO of 0.66 was obtained. Bartlett's test of sphericity indicated that the R-matrix was not an identity matrix and that some relationship between the tested variables could be observed. The test was highly significant (χ^2 (91) = 209.446, $p < 0.001$) and therefore data were presumed suitable for EFA. The determinant value in the correlation matrix was <0.00001 indicating that multicollinearity was likewise not a problem for the data. In other words no highly correlated variables, which could create unstable parameter estimates, were observed.

Communalities indicate the amount of variance in each variable that is accounted for by all factors. As communalities are squared correlations it is expected that they should lie between 0 and 1. Unfortunately, the communality estimates were revealed to be greater than 1 in one or more iterations. This is known as the ultra-Heywood case which has serious implications and renders the factor solution invalid. Factor analysis was therefore not suitable in this instance, and hierarchical cluster analysis was employed instead.

Similarly to factor analysis, hierarchical cluster analysis is a data reduction technique which bands cases or variables (here, tasks) into relatively homologous clusters. At each sequential step of analysis, the case is either assigned to a previously formed cluster or a new cluster is established. The agglomeration schedule reveals how the clusters are progressively formed and the stage at which the two clusters being combined are considered too different to assign within the same cluster (the first large difference in coefficients between two consecutive steps implies the point at which clustering should be stopped). The distance (or the dissimilarity) between the clusters is indicated by one axis of the dendrogram whilst the other axis represents the clusters. Clusters are defined by cutting the dendrogram branches. The cut-off point can be decided upon based simply on the appearance of differences (i.e. where the branches are longer) or with the aid of

statistical/computational methods such as the dynamic tree cut (Langfelder, Zhang, Horvath, 2008).

Hierarchical cluster analysis can be applied using a variety of measures to quantify the (dis)similarity between tasks across participants. Here, the proximities were derived from the correlation table (Table 5.2). Notable interrelationships were observed within and between the explicit and implicit motor tasks with highly significant correlations between all the durations (360ms, 720ms, 1080ms) in the explicit motor task (Interval reproduction – Rep) and to a lesser extent within the implicit motor task (Moving trajectory task – Ball). However, a number of further correlations between tasks are apparent. In regards to the observed pattern of correlations, it must be acknowledged that family-wise error is not corrected for and due to the number of correlations assessed, the $p<0.05$ correlations should be interpreted with a certain degree of caution.

Table 5.2 Intercorrelation measures between all tasks (13 experimental & 1 control task – line length)

	Int 360	**Int 50**	**Line**	**Ball 360**	**Ball 720**	**Ball 1080**	**Rep 360**	**Rep 720**	**Rep 1080**	**TOJ**	**ITD**	**R-R**	**Pulls**
Int 50	.617**												
Line	.049	.121											
Ball 360	.219	.358*	-.033										
Ball 720	.156	-.116	.061	.306									
Ball 1080	.164	.159	.028	.611**	.512*								
Rep360	.524**	.350*	-.086	.424**	.328*	.230							
Rep 720	.384*	.354*	-.030	.517**	.248	.309	.719**						
Rep 1080	.428**	.334*	.000	.382*	.367*	.246	.788**	.620**					
TOJ	.063	.198	-.070	.241	.408**	.430**	.156	.290	.287				
ITD	.064	.123	.000	.275	.053	.325	.086	.306	.172	.185			
R-R	.520**	.333*	-.189	.134	0.32	.140	.320*	.325*	.387*	.110	.198		
Pulls	.256	.029	.061	-.141	.322*	-.060	.128	.154	.132	.286	.133	.204	
Flutter	-.044	.056	-.100	-.150	.079	-.133	-.137	.-229	-.151	.226	-.094	-.145	.227

*p < .05 **p < .01 (two-tailed)

The closest proximity, as can be seen in the below dendrogram (Fig. 5.4) on the left-hand side, can be observed between the explicit motor (interval reproduction) tasks: two of the three durations tested, 360ms (7) and 1080ms (9) form the first clade (r = .788) with the middle task duration (720ms; 8) added at the second stage (r = .669). It is possible that the proximity between the outermost durations, followed by the middle duration at the second stage, is due to the task demands, i.e. the 720ms duration is the mean average duration in this task, a possible reference point, whilst the two more extreme durations might benefit less from internalising/utilising the block average. The same pattern can be noted between the implicit motor tasks with the 360ms (4) and 1080ms (6) forming a cluster first (r = .611) with the 720ms duration added on in the following stage. The

temporal order judgement task (10) forms a clade with these tasks at stage eight (see the middle section of the dendrogram). However, before this, at the third stage of clustering, the two explicit interval discrimination tasks: 50ms (1) and 360ms (2) form a clade (r = .617) with the implicit 'rabid/rapid' language task (12) being added at stage five. It could be that unlike the 'pulls' language task the 'rabid/rapid' task relies only on internal timing and is less affected by other contextual acoustic cues.

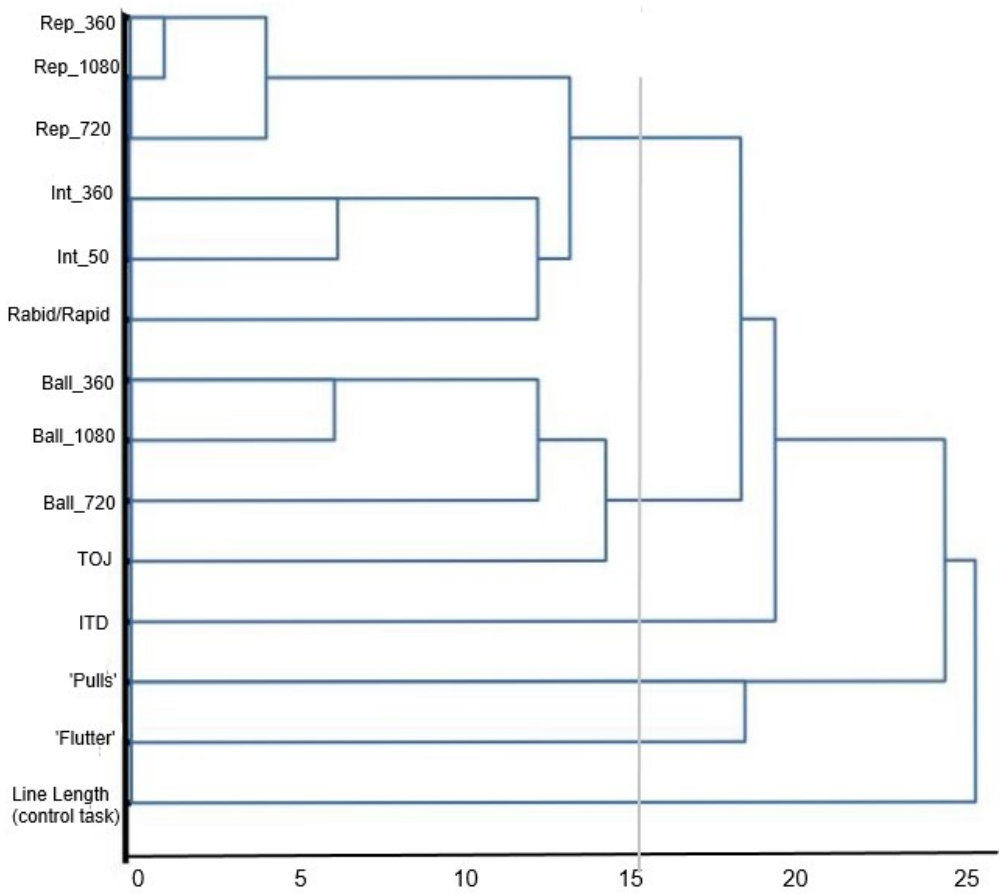

Figure 5.4. Dendrogram clusters for all timing tasks

There is no sudden change in the distance coefficients which would point to an optimal stop for merging clusters, although the largest difference can be noted around stage 5. Looking at the dendrogram, a sensible place to cut the branches appears to be around y = 15, separating the three clusters described so far (explicit motor timing; explicit sensory

timing + rapid/rabid; implicit motor timing) from all other tasks, which each form their own individual clusters. However, another possibility might be to cut the branches around y = 20, forming one large supercluster of timing tasks from the three clusters describe above (plus the ITD task), with a second cluster formed from the pulls and flutter fusion tasks, leaving the control task (3) as an outlier with no association to any of the timing tasks. Additionally it should be noted until a late stage (stage 10), the tasks within each clade correspond to the same category, i.e. explicit-timing vs. implicit-timing with the exception of the rapid/rabid language task which forms a cluster with the interval discrimination tasks at stage 5. (Table 5.3).

Table 5.3. Experimental task and clustering details. The asterisk denotes the only clade which is composed of tasks from differing categories (i.e. explicit and implicit).

Explicit/ Implicit	Task	Stage	Cluster	Task type
E	Int360	1	Rep360 / Rep1080	E+E
E	Int50	2	Rep360 / Rep720	E+E
C	Line length	3	Int360 / Int50	E+E
I	Ball360	4	Ball360 / Ball 1080	I+I
I	Ball720	5	Int /Rapidrabid	E+I*
I	Ball1080	6	Ball360 / Ball 720	I+I
E	Rep360	7	Int360 / Rep360	E+E
E	Rep720	8	Ball360 / TOJ	I+I
E	Rep1080	9	Pulls / Flutter	I+I
I	TOJ	10	Int360 / Ball360	E+I
I	ITD	11	Int360 / ITD	E+I
I	Rapidrabid	12	Int360 / Pulls	E+I
I	Pulls			
I	Flutter			

DISCUSSION

The current experiment investigated the relationship between different forms of timing, with a focus on implicit and explicit timing. A modest association between tasks within each of the two timing types was observed; within each clustering stage the two tasks to form a clade tended to be from a corresponding timing type, with the first exception being the rapid-rabid/ interval discrimination cluster. Port (1978) who investigated how the manipulation of the stop closure duration in the words rapid/rabid affects perception, found that participants directly compare the durations of these two intervals to make their judgement. It is therefore reasonable to infer that the rapid/rabid task demands are very similar to the interval discrimination task and relatively unaffected by any contextual cues. Although papers in the interval timing literature often begin with claims regarding our ubiquitous need to estimate time, this may be counted as possibly the first evidence derived from natural variations in the normal population to support the existence of a common timing mechanism utilised during both speech perception and explicit interval timing. The addition of the control task (line comparison) is not usually included within these type of analyses which further substantiates the observed pattern of results. On this basis it is possible to rule out the notion that the correlations observed here result from other confounding factors pertaining to, for example, individual differences in attention or IQ, thus indicating that the clusters are specific to timing.

Studies comparing the variance of what could broadly be described as explicit and implicit motor timing (tapping and circle drawing) have previously found no correlations in timing variability nor performance across the two tasks amongst individuals, although correlations across certain durations within the tasks were noted (Robertson, Zelaznik, Lantero, Bojczyk, Spencer, Doffin and Schneidt,1999**;** Zelaznik, Spencer & Doffin, 2000; Zelaznik, Spencer & Ivry, 2002; Spencer & Zelaznik, 2003). The motor tasks which were

used in the present experiment differ from the ones utilised in the above studies as the task demands here are more closely matched. The tasks used in the present experiment don't cluster into what could be termed as a supercluster of timing until fairly late, which supports the proposed hypothesis of different mechanisms underlying implicit and explicit timing. Although the clustering of the implicit rabid/rapid language task and the explicit interval discrimination task challenges the idea that implicit timing is a fully separate process.

Ivry, Spencer, Zelaznik and Diedrichsen (2002) distinguish between event based timing which is akin to explicit timing and emergent timing which, as in the case of drawing a circle, arises from the control of the movement trajectory and unlike the former doesn't rely on an internal representation of a time interval. The implicit motor task in the current experiment is quite different from the circle drawing task as participants are simply required to press a button when the stimulus (travelling ball) reaches the target (screen midpoint) and so the task doesn't utilise continuous movement, but there are nonetheless differences in the task demands (relative to the motor reproduction task) which need to be taken into account. Moving stimuli can be affected by certain psychophysical distortions such as for example, the Fröhlich effect (Fröhlich, 1923), since replicated (Müsseler & Neumann, 1992; Kirschfeld & Kammer, 1999; Arschersleben & Müsseler, 1999), which posits that the initial localisation of a moving stimulus by a participant occurs at a later position within the movement and is said to reflect differences in processing times (Metzger 1932). However, cues (flashing of the ball prior to any movement corresponding to the speed at which the ball would travel) which were used in the current experiment, would minimise this bias (Müsseler & Aschersleben, 1998). The flash lag illusion, is another such bias (MacKay, 1958; Nijhawan, 1994). Here, a moving object, paired with a flash is perceived to be displaced slightly further along the path of travel. The effect is noted to persist to the same extent when the flash occurs in an already

moving stimulus as well as when the stimulus is presented on a blank screen simultaneously with the flash just prior to travel (Eagleman & Sejnowski, 2000a; Khurana & Nijhawan, 1995). The most convincing explanation for this bias is offered as an error in localization rather than relative timing (Eagleman & Sejnowski, 2000a; 2000b; 2000c; 2002; 2007) Although is possible that these biases could potentially introduce a source of variability if the bias were to vary from trial to trial, this is unlikely in the current experiment, as for each of the three velocities there is a constant interval of time before the ball crosses the line. Furthermore it is important to note that unlike in the above discussed studies, participants were aware of exactly when the flash would occur which significantly minimises any associated bias. The speed of the flash served to inform the participants of how fast the ball would be travelling and would therefore allow them to calibrate their responses accordingly.

Some neurophysiological evidence also indicates that moving stimuli is processed faster than stationary stimuli (Hoffmann, Stone, & Sherman, 1972; Tolhurst, 1973) and attention modulates the perceived speed of a stimulus (Turattoa, Vescovia & Valsecchia, 2007) to appear to be moving faster. However, despite the additional features of the ball interception task relative to the reproduction task, data from the current tasks suggests that explicit and implicit motor timing may to a large extent rely on the same timer with additional mechanisms contributing to performance in the implicit-domain. Explicit or deliberate timing in a real world situation utilises temporal expectations which interact with expectations about other relevant aspects to form a cohesive sensory perception. In an implicit timing task, timing mechanisms are automatically activated by the temporal element, but deliberate timing expectations can likewise be employed in order to improve aspects of task performance (Jones, Moynihan, MacKenzie, Puente, 2002; Correa, Lupiáñez, Tudela, 2006).

Moving from motor to perceptual timing, Piras and Coull (2011) looked at how performance on explicit and implicit tasks of varying durations conforms to the scalar property (Allan 1979; 1983). Temporal generalisation was used for the explicit timing task (three standard durations; 200ms, 600ms & 1400ms in different blocks) whilst a temporal expectancy task, whereby participants were required to respond as quickly as they could when presented with a target which was preceded by a warning cue by a variable interval, was used to investigate implicit-timing. Prior training was included for both tasks although in the implicit category, the training itself, was utilised to set up temporal expectancies about the time of target onset. The interval between the warning signal and the target was fixed (as in the explicit task; 200ms, 600ms & 1400ms) in order to implicitly generate temporal expectancies in regards to the target onset.. Data from both tasks was observed to follow a U-shaped curve, which the authors interpret as markers of temporal sensitivity. A linear relationship between real and subjective time was likewise observed. Both tasks displayed increased variability as the duration increased, consistent with the scalar property. Although the variance in the 200ms duration, for both tasks was very much comparable, a significant difference was seen at longer durations (600ms &1400ms) whereby the variance in the implicit task was noted to be much higher. The authors conclude that a common mechanism is employed at short durations with different processes contributing at longer durations. Numerous studies have likewise proposed a distinction in the processes underlying sub- and supra-second durations (Rubia, Overmeyer, Taylor, Brammer, William, Simmons, Andrew & Bullmore, 1998; Rammsayer, 1999; Lewis & Miall, 2003b; Buhusi & Meck, 2005; Wiener, Lohoff & Coslett, 2011). Piras and Coull state that their findings indicate that the scalar property holds for both types of timing although there exists a point at which these two forms of timing diverge based on the interval duration. The exact point at which this functional dissociation occurs still remains to be established. Within the current experiment the implicit language task (rabid/rapid) was shown to correlate with the explicit motor tasks

which are based on considerably longer durations, thereby suggesting some commonality between explicit and implicit timing even despite the different durations.

The link between general timing ability and timing in language observed here is supported by a variety of behavioural, neuroimaging and neuroanatomical studies which looked at the temporal envelope in language (e.g. Shannon, Zeng, Kamath, Wygonski, Ekelid, 1995), the importance of accurate timing in speech (e.g. Casini, Burle & Nguyen, 2009) and the neural areas involved in supporting temporal components of speech (e.g. Schirmer, 2004). Patients with a basal ganglia lesion for example, who are impaired in general temporal processing, have likewise been noted to perform poorly on tasks involving the processing of speech segments. Stop consonants, the speech segments used in the rabid/rapid language task in the current experiment, rely on accurate interval perception and unlike the 'pulls' task are not subject to contextual interference. Therefore as mentioned earlier, it is perhaps unsurprising that a strong association between the interval duration discrimination task and the 'rabid/rapid' task was observed. Components of prosody such as frequency, amplitude and duration are used in higher level speech to convey contextual and emotional meaning, so as in the 'pulls' experiment whereby syntactic boundaries are lengthened and then followed by a brief pause to mark a particular boundary tone, they enable the listener to anticipate the syntactic role of an impending speech component. If the prosody is misleading, sentence processing can be disrupted (Steinhauer, Alter, Friederici, 1999). The implicit language ('pulls') task did not appear to have a strong association with any of the other tasks besides a moderate correlation with one variant of the implicit motor task – this could be interpreted to suggest shared processes in motor timing and timing in language. It is likely that the lack of other correlations could be due to the task demands and an interference as a result of contextual cues. Likewise although participants were provided with clear instructions, they were not explicitly instructed on what to base their selection on in each trial as this

would interfere with them making a choice based on whatever cues are naturally used by them.

Deficits in timing have been noted to partially underlie key features observed in disorders such as Parkinson's disease (PD) and Dystonia (Avanzino, Pelosin, Vicario, Lagravinese, Abbruzzese & Martino, 2016). Both motor and perceptual timing appear impaired in PD patients (e.g. Pastor et al., 1992; O'Boyle, Freeman & Cody, 1996; Harrington, Haaland, & Hermanowicz, 1998; Jones, Malone, Dirnberger, Edwards & Jahanshahi, 2008) although results from some recent studies indicate that the same cannot be said for implicit and explicit timing. De Hemptinne, Ivanoiu, Lefèvre & Missal (2012) conducted an implicit oculomotor study where patients were required to visually track a stimulus travelling along a straight path, for either a short (1200ms) or long (2400ms) duration. At the end of its course the target stimulus reversed direction and returned to its original starting point. The reversal resulted in a momentary target lapse and was a notable event which elicited anticipatory eye movements. PD patients were noted to exhibit anticipatory eye movements less frequently but the timing of anticipation of the stimulus motion was statistically the same as that of controls. The authors therefore suggest that implicit timing of salient events remains unaffected in PD patients. The opposite effect has been observed in Dystonia, a neurological movement disorder which appears not to affect explicit motor timing (Van der Steen, VanVugt, Keller & Altenmüller, (2014) but patients instead display selective implicit timing impairments (Avanzino et al., 2013; Martino et al., 2015). Results here point to similar inconsistencies, with overlap between some, but not all, implicit/explicit timing tasks.

Correlation and principal factor analysis was previously used to assess performance and look for commonalities in timing in a study which utilised eight tasks, including; temporal generalisation, rhythm perception, duration discrimination, TOJ as well as

auditory flutter fusion (Rammsayer & Brandler, 2004). It was noted that 32% of the variance from these tasks could be accounted for by one factor which suggests that to a certain extent a shared mechanism for timing underlies these timing behaviours. Auditory flutter fusion (AFF) did not load onto any factors, so despite the different analyses, the findings are in line with the results of the current study. The authors note that this may be due to the task relying more on aspects of auditory processing rather than interval duration as is the case with the other tasks (Florentine & Buus, 1984). This claim is further supported by evidence from neuropharmacological studies which found that AFF remained unaffected by the administration of Haloperidol which affects dopaminergic activity (Rammsayer, 1989). Dopamine has been found to play a substantial role in interval timing in both humans and animals (e.g. Rammsayer, 1993; 1997; Drew, Fairhurst, Malapani, Horvitz & Balsam 2003; Matell ,Bateson & Meck, 2006; Cheng, Ali & Meck, 2007; Jones and Jahanshahi, 2009; Coull et al., 2011; Meck, Cheng, MacDonald, Gainetdinov, 2011; Caron MG, Cevik Jones & Jahansahi, 2014; Bermudes & Schults 2014) and it is therefore assumed the as in the above study, the *flutter* task in the current experiment does not form a cluster with any of the other tasks because of fundamentally different mechanisms, rather than simply scale differences in duration. The results from the inter-aural time difference task provide a similar sanity check. The ITD is interpreted by the brain (for the purposes of decoding direction) by a specialised delay-line mechanism in the medial superior olive (Kandel, Schwartz & Jessell, 2000), and as such is very unlikely to show substantial overlap with long-interval timing mechanisms, as observed here.

As discussed in the introduction section of this chapter, the timing of different durations has been suggested to be governed by distinct mechanisms. The results of the current experiment do not substantiate this difference, as tasks were often observed to correlate despite marked differences in duration, as can be seen for example with the duration

discrimination task (50ms) which revealed significant correlations with the explicit motor task at all durations including the 1080ms duration. The data to some extent support the claim made by Rammsayer & Ulrich (2005) who suggest that the same processes are involved in sub- and supra-second timing. The authors note that previously observed discrepancies are a result of attention-based mechanisms and task demands. Interestingly the implicit language task *rabid/rapid* which is based on very short durations was also observed to correlate with the explicit motor task as well as the duration discrimination tasks at all durations. Timing in language is therefore assumed to rely at least to some degree on the same underlying mechanism as other temporal behaviours. The distinction between explicit and implicit timing appears to otherwise hold as all the tasks within the battery formed initial clusters based on their type (explicit vs. implicit). The results of the current experiment correspond to the findings by Merchant et al (2008) as discussed in the introduction, who suggest that the difference between explicit and implicit timing is better defined than distinctions in modality and task demands.

In summary, different timing behaviours are here suggested to be supported by different mechanisms with a common global mechanism which acts at particular stages of timing which would account for the correlations and the forming of clusters at the later stages. The possibility of independent mechanisms which nonetheless possess a significant overlap should be considered, as a correlation can arise for a variety of reasons (e.g. a very low-level neural property, such as temporal reliability of action potential conduction, which might support disparate mechanisms across the brain).

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CHAPTER 6 – CONCLUSION

The overall focus of this thesis has been on the temporal processes underlying interval timing. An investigation of the functional architecture was attempted through a number of established and novel experimental procedures. In this chapter, I will briefly summarise the results from my four experimental chapters, and then revisit an issue that dominates current theoretical positions on interval timing – whether there is a single scalar timing system controlling all timed behaviours.

6.1. Summary of the current experiments

Numerous models of interval timing have attempted to describe the underlying mechanisms which enable our ability to estimate durations in a wide range of contexts and behaviours. Pacemaker-accumulator type models suggest that timing is governed by an internal clock akin to a stopwatch, which like the device, can be started, paused and stopped at will. The first experimental chapter in this thesis sought to explore this notion by employing a modified interval discrimination task. Participants were required to compare a single standard interval with the total sum of another split interval. The experiment investigated how the predictions made by the ACT-R model would compare with the observed results. The ACT-R model posits a gradually slowing pulse rate in line with increasing durations, therefore in addition to measuring variable performance error, accuracy was another aspect considered in the investigation. The observed precision was considerably worse than predicted by the model and a shift in accuracy whereby the split-intervals were reported as longer rather than shorter (as would be the case with a slowing pacemaker) was also observed. Findings from this study indicate that counter models such as the investigated clock module in its current form cannot simply be paused during

timing. Other models of interval timing such as the multiple-oscillator models are therefore better able to account for these data.

The scalar property widely observed in timing research refers to observed variable errors in temporal estimation, which are noted to increase linearly with the timed duration. The experiment presented in Chapter 3 aimed to investigate the validity of Weber's Law (more specifically its generalised version) to describe the timing of interval durations. In line with previous studies which have suggested that systematic deviations from this Law for time may arise only with considerable training (Kristofferson, 1980), extensive practice was undertaken across a set of eight durations ranging from 71ms to 1131ms. Two different tasks were employed so as to ascertain that any observed violations are not an artefact particular to any task. Although coinciding deviations from Weber's Law at specific durations for two of the three participants were observed, these were not echoed in both of the tasks to a statistically reliable degree.

Transfer of learning in the perceptual domain is widely documented, and similarly timing research has utilised this technique in order to gain further insight into temporal processing across different durations and modalities. Although a number of interval timing studies have employed this methodology, the experiment described in Chapter 4 attempted to broaden the scope by including a wide range of tasks and durations not previously investigated. Certain constraints pertaining to generalisation have been reported in the timing literature, which were kept in mind for the purpose of the study design. Extensive training on an auditory interval discrimination task was undertaken by three participants over a period of two months. Transfer of learning to a range of other tasks was then assessed. The observed findings point to a certain degree of temporal specificity in the timing of short and long durations and a distinct overlap between motor and perceptual timing mechanisms.

The most frequently employed paradigm in timing research requires participants to explicitly attend to a presented interval duration, after which a comparison (or reproduction) of the duration can be made. However in real life situations, accurate timing is a crucial component of many non-temporal behaviours. Chapter 5 sought to explore the relationship between these two forms of timing in addition to a number of previously proposed dichotomies. A battery of tasks composed of explicit and implicit measures, with a further subdivision of motor and perceptual tasks, over a wide range of durations was employed. Particular attention was paid to language which relies heavily on a temporal component. Two language tasks were included in the set - a novel task using temporary sentence ambiguity based on phrase final lengthening, as well as a modified version of a previously used task relying on a phonetic feature – voice onset time. A significant relationship between the latter task and several of the motor and perceptual tasks was observed suggesting a possible overlap of timing processes. Correlations between several of the motor and perceptual tasks, including tasks utilising different durations, were also noted. However to a large extent, a divide between the implicit and explicit tasks was discerned.

Does a single, scalar, timing system control all timed behaviours in humans?

Weber's Law, a fundamental property in the study of sensory processing, describes the relationship between stimulus magnitude and sensory discrimination. The neural basis underlying this psychophysical observation has not yet been fully established although studies suggest that Weber's Law is a reflection of the variability observed in a neuronal spike train (Kang, Wu, Smerieri, Feng, 2010). The sensory threshold of a stimulus pertains to the lowest stimulus strength which can be detected by a subject. A change in the stimulus amplitude changes the activity of sensory receptors, larger receptor potentials will be evoked as a result of a more pronounced or detectable stimulus which

then in turn generates higher frequency action potentials. A sensory threshold is dependent on two factors; the absolute detectability of the stimulus and the criterion which is used to determine its presence. The latter also accounts for any bias in response to a psychological or pharmacological influence (Gardener & Martin, 2000).

The ubiquity of Weber's Law in sensory processing has sometimes been challenged, but these deviations are usually attributed to excessive noise from non-sensory components or sensory processing capabilities. For example, tit's been suggested that the variability associated with visual coding for action (in this case adjusting one's hand to grasp objects of increasing size) violates Weber's Law (Ganel, Chajut & Algom, 2008; Utz). However, a later study found that the widely used measure in many action-perception studies introduces additional factors which act in opposition to the influence of sensory laws and conceal the effect on the grasping response (Hesse, Aschenneller & Schenk, 2015). In other studies relating to animal behaviour, a near-miss version of Weber's Law was found to be a better fit rather than the standard version for nectar feeding animals (bats, hummingbirds, honeybees, and bumblebees) in regards to sugar discrimination, this was explained due to the different sensory processing abilities found in different animal species (Nachev, Stich & Winter, 2013). As discussed in the previous chapters, the scalar property, a general form of Weber's Law is a prominent feature in the study of interval timing.

A critical feature of SET, one of the most influential interval timing paradigms of the past few decades, is it's adherence to the scalar property (Gibbon, 1977; Gibbon & Church, 1990). The flexibility of the model has allowed for many adaptations and timing errors have been attributed to different clock components (Killeen & Taylor, 2000; Rammsayer & Ulrich, R, 2001) or processes such as attention (Grondin & Rammsayer, 2003; Gamache, Grondin, & Zakay, 2011) and memory (Grondin, 2005). Various studies in

timing literature have observed interval timing to comply with a generalised form of Weber's Law (e.g. Killeen & Weiss, 1987; Malapani & Fairhurst, 2002; Wearden 2003; Buhusi Aziz, Winslow, Carter, Swearingen & Buhusi, 2009). Time-scale invariant timing has also been observed in a variety of species and findings from psychophysical studies have to an extent also been substantiated in investigations employing differing approaches such as lesion (Meck, Church, Wenk & Olton, 1987) and pharmacological studies (Buhusi & Meck, 2002).

An investigation by Merchant, who used both interval discrimination and production (single and multiple tapping) tasks in the visual and auditory modality, found an adherence to Weber's Law in all tasks and durations. Although it must be noted that the six durations which were employed in the study ranged from 350ms to 1000ms, which as discussed in Chapter 3, is within a range generally found compliant with Weber's Law. Further analysis also revealed considerable differences in variability between tasks and modalities with larger variability observed in perceptual tasks as opposed to the motor tasks – this finding could likewise shed some light on the generalisation to the motor tasks despite some participants not displaying significant learning effects on the trained durations in the interval discrimination task (Chapter 4). Although the set of durations used in the present experiment (Chapter 3) utilised a wide range of durations including ones below and above this range, deviations for two of the participants were nonetheless observed between the 566ms and 800ms point. It is possible that a clearer picture might be obtained with a larger sample however observations in timing literature have at times revealed robust deviations from Weber's Law, which could not be accounted for by any failings in methodology (e.g. Madison, 2001; Grondin, 2003; Grondin & Killeen, 2009). The results obtained in the present set of experiments, together with findings from previous studies, could be tentatively interpreted to suggest some inconsistencies, ones which clock models such as SET are not able to fully account for.

The inclusion of the scalar property has been noted to place some limitations on models of interval timing, and according to an information theoretic argument utilised by Hass and Hermann (2012), the neural basis of timing processes has to rest on increasing variance in order to accurately reflect these observed scalar errors. A number of models such as BeT (Behavioral Theory of Timing; Killeen & Fetterman, 1988) or LeT (Learning to Time; Machado, 1997) do not require an adherence to Weber's Law. LeT predicts non-compliance with Weber's Law which comes about as a result of learnt associations during the acquisition of intervals in temporal discrimination (Machado and Keen, 1999 Machado and Guilihardi, 2000). However, this model in turn, is not able to account for many other observed results (e.g. Whitaker, Lowe & Wearden, 2003; Whitaker, Lowe & Wearden, 2008). SET has been a highly influential and adept model of interval timing, able to account for a variety of timing behaviours although violations of the scalar property suggest that in its present form it is not a complete depiction of timing processes.

More recent adaptations, such as the ACT-R model have incorporated the clock module into a previously described cognitive architecture. This allows for a more complete explanation insofar the interaction between timing and other cognitive components is concerned. The clock module nonetheless functions in a stand-alone capacity, and so could potentially be replaced by another module which allows for the same timing behaviour. Similarly to other pacemaker models, temporal estimates equal the amount of pulses stored in the accumulator although in this instance, the breaks between the pulses gradually increase which enables the scalar property to emerge without the need for any further ad hoc additions. Pacemaker-accumulator models generally provide a good account of a subject's behaviour when discriminating between two intervals. Likewise, data from several studies (Fortin and Massé, 2000; Tremblay & Fortin, 2003; Fortin & Tremblay, 2006; Fortin et al., 2009) has to an extent supported the notion that a subject is able to accurately time a broken interval, this behaviour being accounted for by the

pause/restart component of counter models. Unlike in the above noted studies, the focus of the initial experiments (discussed in Chapter 2) which tested the SET model, was on precision which would allow for a more stable and systematic analysis. Accuracy in timing research, as already mentioned, is prone to considerable shifts in response to experimental manipulations.

The additional amount of nonscalar variance required for this 'pause' (i.e. opening and closing of the switch) was calculated, bearing in mind a participant strategy most facilitating towards the model. Nonetheless the observed deterioration in performance far exceeded the predictions suggesting that the SET model is not able to account for this timing behaviour. Subsequently, Chapter 2 assessed the ACT-R model with its gradually decreasing pulse rate. Here, in addition to a comparison between the whole and split-interval tasks, another facet was considered – the premise of the split interval being perceived as shorter when compared to an unbroken interval. This prediction follows on from the declining pulse rate postulated in the model, which would result in a lesser accumulation of pulses in the second part of the split interval. However, contrary results were observed, with participants estimating the target interval to be longer, rather than shorter than the standard. Even discounting this shift in accuracy, the increase in variability, similarly to SET was not accounted for well by the ACT-R model.

A recently developed model – the coupled excitatory-inhibitory oscillation model (EIO; Gu et al, 2015), similarly to the ACT-R model, considers timing in a more comprehensive manner as far as its relation to other cognitive processes is concerned. A variety of observations have suggested an interaction between timing and memory, which is a key component of the model. Shared neural processes have been implied as a result of the noted interference observed between working memory and timing (Fortin & Rousseau, 1998) often in the form of a positive correlation, whereby an increase in working memory

demands reduce the accuracy in temporal tasks (e.g. Fortin et al, 1993). Furthermore, significant associations between subjects' interval timing performance and working memory capacity even when other factors such as intelligence have been controlled for, have also been documented (Broadway & Eagle, 2011; Woehrle & Magliano, 2012). Activation of neural regions in both timing and memory has likewise been observed in the dorso-lateral prefrontal cortex (Wager & Smith, 2003; Lustig, Matell & Meck, 2005; Genovesio, Tsujimoto & Wise, 2006), which further substantiates the notion of an interplay between timing and working memory.

Unlike many other models which account predominantly for a particular segment of observations in the interval timing literature, e.g. behavioural (e.g. Gibbon, 1977; Killeen & Fetterman, 1988) or neuronal dynamics (e.g. Durstewitz, 2003; Kitano, Okamoto, & Fukai), the EIO model attempts to bridge the gap and considers a wide range of anatomical, neurophysiological, pharmacological, and behavioural data in order to provide a more complete account of interval timing. The 'clock' in counter models requires a separate signal to start timing after which the estimate or number of pulses are passed to a short term memory store, where a comparison can then be made. Within the EIO model, which nonetheless incorporates elements from traditional accounts such as SET, the timing process does not necessitate an active comparison, rather the encoding of stimuli which prompts an onset in interval timing, automatically triggers the phase-locking of cortical neurons, monitored by medium spiny neurons in the striatum. Similarly to the SBF model discussed in Chapter 2, performance in the split-interval task in the context of EIO would be expected to deteriorate below the level specified by counter models.

Dedicated models of timing such as the pacemaker-accumulator class of models suggest that timing irrespective of modality or duration is governed by a single clock. No

analogous neural mechanism has been pinpointed, although the pre-supplementary motor area was suggested to act as the accumulator component of the clock (Coull, Cheng & Meck, 2011). This notion was based on electrophysiological findings, whereby the contingent negative variation (CNV) said to emanate from the pre-supplementary motor area was suggested to vary in accordance with a timed duration (Macar, Vidal, Casini, 1999), although later studies did not replicate this finding (Kononowicz & Van Rijn, 2011). Other constituents of the clock and integral processes which make up the model such as the noted ratio comparisons are not accounted for, although it is possible that the neural substrates could still be identified.

Intrinsic models, by contrast, suggest that timing is inherent in the neural dynamics with different timing behaviours and durations relying on distinct processes. This hypothesis is more in line with the various dichotomies observed in different timing behaviours. One of the most frequently encountered notions in that regard, is that of disparate mechanisms governing the timing of short and long interval durations. This observation is supported by data from numerous psychophysical, genetic and imaging studies (e.g. Rammsayer 1994; 1997; 1999; Breukelaar & Dalrymple-Alford 1999; Lewis & Miall 2003a;,b; Wiener, Lohoff, & Coslett, 2011). Differences in learnability between short and long durations further substantiate this hypothesis. A study by Brandler and Rammsayer (2001) for example, found improvement in both short (50ms) and long (1000ms) intervals after two training sessions and continued enhancement in the long durations with further training, but continued training on the short durations did not reveal the same pattern, as performance was noted to reach a plateau. In line with the sensory integration hypothesis, the authors considered that the disparate results observed after extended training could be related to non-temporal elements such as participant adjustment to the task, as well as a reliance on particular stimulus characteristics as in the use of additional strategies, employed when longer intervals are being discriminated. These cognitively mediated

strategies (Grondin, Meilleur-Wells & Lachance, 1999) would not be advantageous to the more sensory mediated timing which is said to be utilised in millisecond durations. However the likelihood thereof was not supported in their next experiment, whereby the effect of the utilised stimuli was investigated in order to ensure that participants are not employing non temporal stimulus characteristics in their discrimination. The observed results were therefore asserted to be a result of different mechanisms underlying the timing of short and long durations. Temporal specificity, in regards to distinct mechanisms governing the timing of different durations was to an extent supported in the present experiments (Chapter 4) whereby improved performance was observed on a subset of trained intervals in the transfer of learning experiment.

The multimodal processing of temporal information which elucidates on the underlying mechanisms of timing has likewise been investigated via transfer of learning studies. Although a considerable amount of experiments relying on this methodology have been conducted, for the most part it is not one which is most frequently employed in timing research. This may partially be due to the labour intensive nature thereof as well as the sometimes considerable influence of other factors. Important considerations pertain to the training itself; the schedule, the tasks employed and the amount of training which is undertaken, as these have all been observed to have a significant impact on whether generalisation takes place. Although not extensively researched in timing literature (as far as I am aware), the level to which more general perceptual learning takes place also differs between individuals, this may be due to physiological or other individual differences (e.g. Goldstone, 1998; Wong, Peters, Goldreich, 2013) and so it stands to reason that this could likewise be a significant factor in temporal research.

The primary finding of the present transfer of learning experiment (Chapter 4) was the observed transfer from perceptual to motor learning which suggests a common

mechanism underlying these timing behaviours. Generalisation from perception to action and vice versa has not been extensively studied in temporal research although the current results are in line with those of previous studies (Meegan et al, 2000). An important consideration in transfer between motor and perceptual tasks pertains to whether generalisation between these tasks is specifically a reflection of shared mechanisms. This is due to the sensory component which is present in motor tasks such as in the interval reproduction paradigm whereby participants first hear the interval and then reproduce it with their fingers. But this sensory component is significantly lessened in tasks such as the tapping tasks where transfer was likewise observed.

The subsequent experiment (Chapter 5) sought to substantiate these findings in addition to further exploring the suggested dichotomies and relationships between different timing behaviours and durations. Once again the most salient observation were the significant correlations between the explicit motor task (interval reproduction) and the interval discrimination tasks, these were observed at all of the employed durations (50ms & 360ms – interval discrimination and 360ms, 720ms & 1080ms – interval reproduction). Correlations between the 360ms interval discrimination task and the motor tasks were observed to be stronger than those with the 50ms interval discrimination task. The association between the 50ms perceptual and the 1080ms motor task, albeit not particularly high, could still be seen to undermine the previously mentioned temporal specificity of sub- and supra-second durations. However it must be emphasised that the noted divide between the timing of short and long durations is not defined by a strict boundary or 'break point', as ascertained by Lewis & Miall (2003) in their meta-analysis and it is instead noted to be a gradual trend.

Neuroimaging studies have identified a number of regions which appear to be involved in both motor and perceptual timing, these include the pre-supplementary motor area, the

dorsolateral prefrontal and the inferior parietal cortices (Schubotz, Friederici & von Cramon, 2000; Rao, Mayer & Harrington, 2001; Coull, Vidal, Nazarian, & Macar, 2004; Pouthas et al. 2005; Tregellas, Davalos & Rojas, 2006). The cerebellum has likewise been implicated in sub-second timing for both interval discrimination and production (Bueti, Walsh, Frith & Rees, 2008). Comparable variability in motor and perceptual tasks has also been documented in behavioural studies (e.g. Keele, Pokorny, Corcos, & Ivry, 1985; Ivry & Hazeltine, 1995). A significant amount of data therefore points to shared or at least partially overlapping mechanisms involved in motor and perceptual timing.

Another striking observation in the hierarchical clustering experiment (Chapter 5) was the association between the explicit motor and interval discrimination tasks with the perceptual language task (the rapid/rabid task). It is possible that certain overlap between these forms of timing is present. Schubotz et al. (2000) conducted a fMRI study which compared the neural regions involved in time perception and those implicated in temporal planning and coordination of movements. Participants were required to identify deviants in a presented auditory segment in addition to pinpointing a deviant in another visually presented task (patterns which 'moved' at particular rates over successive frames in order to create a rhythm, as mentioned in Chapter 1). Corresponding activation was observed in several regions in addition to the frontal opercular cortex which has conventionally only been ascribed to speech and language. However tongue movements not related to speech as well as imagined finger movements also display activation in the operculum (Fox, Petersen, Posner & Raichle, 1988). Broca's region localised in the opercular portion of the inferior frontal cortex, has further been implicated in time-dependent motor and perceptual processes concerned with verbal and nonverbal communication (reviewed by: Nishitani, Schürmann, Amunts, Hari, 2005) as well as the perception of music (Brown, Martinez & Parsons, 2006). These briefly mentioned neuroimaging studies support the data in the present experiment (Chapter 5) whereby it is likely that the neural substrates

of timing in language to some extent overlap with other forms of timing. An important component of the presently discussed chapter, was the distinction between explicit and implicit timing, this dissociation is believed to be in line with numerous other observations documented in timing literature. Neuroimaging studies have found activation in a wide range of neural regions whilst employing explicit and implicit tasks and these substantiate behavioural observations which indicate considerable differences between these forms of timing. Present results indicate that the distinction, as previously mentioned, is better defined than those proposed between other forms of timing.

The findings from the set of experiments in this thesis have attempted to add to the current knowledge in the field of interval time perception. A study, like the one detailed in the first experimental chapter, whereby the implicit predictions made by counter models using sub-second durations are investigated has not previously been presented. The results indicate that counter models although able to account for a wide range of timing behaviours are nonetheless not able to account for 'paused' timing in their current state. The results of the following chapter (examining deviations from Weber's law) were not conclusive; despite deviations at certain durations being observed, these were not replicated in both tasks. However a number of other studies observed deviations from Weber's Law and it is necessary to try and understand the source and meaning of the non-constant Weber Ratio. Whether Weber's Law holds for different interval durations is an important question which could be an indicator of different timing mechanisms additional to the scalar property.

Although a number of studies have employed the methodology described in chapter 4, the experiment attempted to broaden the scope by including a wide range of tasks and durations, previously not investigated. Significant associations between motor and perceptual timing were observed which in addition to a number of other studies discussed

within the chapter suggest an overlap between motor and perceptual timing. This finding was likewise observed in the following chapter which relied on measuring correlations rather than transfer of training. Finally timing in language which has not been investigated in much detail, in regards to its association with other forms of timing, was included in a large battery of tasks and the results indicate that there is some overlap between the different forms of timing behaviours in conjunction with timing in language. The set of experiments conducted in this thesis often rely on correlational analysis and the limitations pertaining to this type of analysis are acknowledged. Nonetheless by using control tasks and control participants many of the confounding factors are eliminated.

The majority of the current models described in the interval timing literature do not as yet appear to fully account for all timing behaviours. It is unlikely that interval timing is governed by a single clock, rather an interplay of a number of distinct timing processes which nonetheless overlap at particular stages is proposed. At present, the observed results seem more in line with the oscillator type as opposed to the more traditional pacemaker-accumulator type models. Confounding elements pertaining to task characteristics and other aspects related to the used methodology in the timing literature as well as in the present set of experiments, although no doubt a factor, do not discount the observed dissociations as far as the timing of different durations and certain behaviours is concerned. A strong indication of an overlap between motor and perceptual timing as well as the association of language to other forms of timing is nonetheless suggested. Although the findings from the current study do not fully support a strict boundary between the timing of different durations, the possibility thereof is also not entirely excluded.

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